Flora of the Ravenscrag Formation of the Big Muddy Valley, Willow Bunch Lake Map Area (72H), Saskatchewan

A Thesis

Submitted to the College of Graduate Studies and Research

in Partial Fulfillment of the Requirements

for a Degree of Master of Science

in the Department of Geological Sciences

University of Saskatchewan

Saskatoon

Andrew C. L. Postnikoff

Spring 2009

ABSTRACT

Paleocene aged beds of the Ravenscrag Formation exposed in the Big Muddy Valley of Southern Saskatchewan produce numerous plant fossils. Studies into these fossils last occurred in the 1930s. Studies into the contemporaneous Ravenscrag Butte flora of southwestern Saskatchewan have shown that the flora of these beds needed updating. Collections of specimens and stratigraphic sections were taken from the area.

Forty species, including two new species and seven unknowns were identified. *Elatocladus megasequoiae* n.sp. and *Corvirupestrobus adrielensis* n.sp. are both Conifers, and *Corvirupestrobus* is also a new genus. Many species were previously unknown in Ravenscrag Formation floras, including cf. *Lygodium* sp., *Thelypteris* sp., *Sparganium* sp., *Paloreodoxites plicata* (Lesquereux) Knowlton, *Carya antiquorum* Newberry and *Nordenskioldia borealis* Heer. Two new combinations are proposed, transferring *Quercus praegroenlandica* Berry to *Fagopsiphyllum praegroenlandicum* (Berry) n. comb. and *Harmsia hydrocotoloidea* McIver and Basinger to *Harmsvernia hydrocotoloidea* (McIver and Basinger) n. comb., with *Harmsvernia* a new genus.

Three sub-floras are recognized for this flora. Sub-flora 1 is a conifer dominated swamp sub-flora, common to many Paleocene localities. Sub-flora 2 is a conifer dominated sub-flora suspected of being from a drier environment than florule 1. Elements of sub-flora 1 appear in sub-flora 2 and vice versa, but relative abundances differ. There is little taxonomic overlap between sub-floras 1 and 2 with sub-flora 3. Sub-flora 3 is more typical of contemporaneous localities to the south such as those of the Bear Den Member of the Golden Valley Formation (Hickey 1977), whereas sub-floras 1 and 2 are more typical of northern localities, like the Genesee locality

(Chandrasekharam 1974) and Koryak Formation (Golovneva 1994). The Big Muddy Valley occurs at the ecotone between the Arctic floras and the floras of the South.

The taxonomy of *Glyptostrobus* from the Paleocene is revised as an appendix, written as a separate report. This revision is more extensive than for the other taxa of this study, utilizing materials from numerous other localities, including the Joffre Bridge Roadcut localities (Hoffman and Stockey 1999), the Smokey Tower localities (Christophel 1976) and the Buchanan Lake Formation (Basinger 1991).

ACKNOWLEDGEMENTS

The author is grateful to Dr. J.F. Basinger, who initiated this project, and provided supervision and support through the many aspects of its preparation. Dr. H. Cota-Sanchez and Dr. R. Renault are thanked for serving as the supervisory committee, and Dr. A. Davis for temporarily stepping in when Dr. Cota-Sanchez was on sabbatical.

This project would not have happened without the input of Mr. A. Larson, a paleontological enthusiast and retired science teacher from Bengough Saskatchewan, who provided the impetus for Dr. Basinger, collecting many fossils and identifying the majority of the collecting localities, as well as opening up his collections to complete our understanding, and introducing us to the local community.

The author wishes to thank his field assistants, A. Csank, S. Postnikoff, B. Postnikoff, L. Postnikoff and D. Lindsay, who contributed on the numerous trips that occurred in 2003, 2004, 2005 and 2006. Also, the author wishes to acknowledge their support when not in the field. This project would not have been possible without them.

Thanks go to D. Postnikoff, and S. and M. Manchester for opening their homes to the author during conferences to present the information from this project. Being able to stay with friendly people makes traveling much more rewarding, if for no other reason than not needing to spend $100 a day for a place to sleep.

Funding was provided for portions of this project from the University of Saskatchewan, NSERC (through grants held by Dr. Basinger), The PCSP, and the BSA.

Dedication

To the memory of Dr. E.E. McIver, who was instrumental in the origins of this project, both in providing a framework and understanding to be followed through her work on the flora of Ravenscrag Butte, and also providing early opportunities to get the author exposure to the field. Without access to arctic sausages and drake hams, the chance that the author would have entered the field would have been lessened.

To the spirit of academic camaraderie expressed in the formation of the Gordo spirit fostered at Laguna Del Hunco. May the legend grow.

To Dr. Y. Liu for his advice to abandon palaeobotany because there is no money in it. One must remember that palaeobotany is something that only the privileged few get to participate in, making all drudgeries and difficulties of this field bearable. One must love the field, otherwise there is no reason to stick with it.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

NSERC	National Science and Engineering Research Council
PCSP	Polar Continental Shelf Project
BSA	Botanical Society of America
GSC	Geologic Survey of Canada
US	University of Saskatchewan Palaeobotanical Localitiy numbers
USPC	University of Saskatchewan Palaeobotanical Collection
RSM	Royal Saskatchewan Museum
MAT	Mean Annual Temperature
LMA	Leaf Margin Analysis
CLAMP	Climate Leaf Analysis Multivariate Program
NLR	Nearest Living Relative
CA	Coexistence Approach
USDA	United States Department of Agriculture
BIP	Brito-Arctic Igneous Province

CHAPTER 1
INTRODUCTION

There is a long history of studies into the late Cretaceous and Paleocene floras of the Great Plains, and in particular the Williston Basin, beginning with J.W. Dawson's reports of the late 1800s (Brown 1962). Following the initial reports of regional palaeobotany and detailed geology, the early 1900s featured broad overviews of the area, characterized by wide-scale exploration and mapping. Many extensive monographs were produced during this time, concerning both the paleofloras and the geology of this region, which covers parts of Alberta, Saskatchewan, North Dakota, South Dakota, Montana, and Wyoming, and additional adjacent areas, depending on the author. Three monographs stand out in the study of Ravenscrag Formation floral materials. E. W. Berry's (1935) report on the flora of the Whitemud Formation and Ravenscrag Formation uniquely included a floral list of the Willow Bunch Lake map area. W. A. Bell's (1949) report on similarly-aged floras of western Alberta provides a different taxonomic model, but one worth considering. R. W. Brown's (1962) posthumous monograph culminated his life's work, and is considered the end of the period of extensive monographs. The latter is widely considered the primary palaeofloral list for the time period and region, even though members are slowly being revised to reflect new understanding (S.R. Manchester, personal communication 2004). One monograph stands out geologically for the study area, the "Geology of Southern Saskatchewan" (Fraser et al. 1935). Additional studies have been published on the economic potential of the region; primarily assessing clay resources (Hudson 1987) and coal (Broughton 1978; Potter et al. 1991; Sweet 1993).

Subsequent studies into the flora and geology of the Paleocene of the Western Interior developed in two directions. In contrast to the initial sweeping monographs, many workers focused on detailed investigations on individual or small sets of closely linked localities. Studies in Alberta included the Smokey Tower locality (Christophel 1976), the Genesee locality (Chandrasekharam 1974), and the Joffre Bridge road-cut

locality (Hoffman and Stockey 1999). The Cypress Lake map area of southwestern Saskatchewan has received a few paleofloral studies (McIver and Basinger 1993; McIver 2002). Extensive work has been undertaken in the United States as well, including reports on the Upper Paleocene Golden Valley Formation (Hickey 1977), the lower Paleocene Fort Union Group (Bown et al. 1994; Crane et al. 1990; Gemmill and Johnson 1997; Johnson 2002), and Maastrichtian Hell Creek Formation (Johnson 1996; Johnson 2002; Johnson et al. 2003). A number of floras have also been documented from the synchronous adjacent Denver Basin (Barclay et al. 2003; Johnson and Ellis 2002; Johnson et al. 2003; Raynolds and Johnson 2003; Ellis et al. 2003).

In addition to these studies, which often contained taxonomic debates in the discussion of their floral lists, a series of papers have focused specifically on properly understanding individual taxa. S. R. Manchester is the most prolific author tackling these taxonomic problems, having published on the Betulaceae (Manchester and Chen 1996, 1998; Manchester and Guo 1996), *Davidia* (Manchester et al. 1999; Manchester 2002), *Celtis* (Manchester et al. 2002), the Junglandaceae (Manchester 1987; Manchester and Dilcher 1997), *Aesculus* (Manchester 2001) and the Platanaceae (Manchester 1986; Kvacek et al. 2001; Kvacek and Manchester 2004). Additional works include studies on the Betulaceae (Sun and Stockey 1992), *Trochodendroides-Nyssidium-Joffrea* complex (Crane 1984; Crane and Stockey 1985), Trochodendraceae (Pigg et al. 2007), Lemnaceae (Stockey et al. 1997), *Quereuxia*/*Trapago* (Stockey and Rothwell 1997; Hickey 2001), *Mesocyparis* (McIver and Basinger 1986; McIver and Aulenback 1994), *Azolla* (Hoffman and Stockey 1994) *Equisetum* (McIver and Basinger 1989) and *Fokienia* (McIver 1992).

Finally, some workers have synthesized the geological and floral information gathered in the previous papers and generated encompassing theories. These papers often focus on paleoclimatic interpretations, based, for example, on utilizing leaf anatomy climate evaluation (Wolfe 1990; Wilf and Johnson 2004). These investigations utilize non-traditional pseudo-taxonomy, where leaves with differing morphologies are treated as separate taxonomic entities. This is despite the acknowledgement that some of these leaves are recognized as likely representing different growth types within one species, such as shade leaves versus sun leaves (Wolfe 1990).

Study of the biostratigraphy of this time in Earth history has been augmented by extensive scientific and public interest in the K-T boundary. The Western Interior provides terrestrial fossils from both below and above the K-T boundary, facilitating an understanding of changes that occurred in a terrestrial setting at the end of the Cretaceous, and how the ecosystems responded. To clarify the timing of terrestrial biostratigraphy of the Great Plains, a number of projects are ongoing (Lerbekmo 1985; Bown et al. 1994), including palynological surveys of individual localities and the greater region (Sweet 1978; Sweet and Cameron 1991; Demchuk 1990; Kroeger and Steadman 1990; Braman and Sweet 1999), and correlations utilizing fresh water molluscs (Lerbekmo 1985, Hartman and Kirkland 2002) or mammals (Bown et al. 1994; Pearson et al. 2002). In addition to relative dating of the strata, absolute dating has been attempted by magnetostratigraphy (Hicks et al. 2002; Hicks et al. 2003; Wilf and Johnson 2004), a technique utilized when other absolute time data points are known, such as the terminal bolide impact event distinguishing the Cretaceous-Tertiary (K-T) Boundary. The magnetostratigraphic bands combined with knowledge of the K-T boundary datum can limit the earliest Paleocene time to a few hundred thousand years. Volcanic deposits, conducive to radiometric dating, are rare but present in a few localities (Hartman and Kihm 1990). Synthesizing the evidence from these various sources has resulted in confident timing of paleo events in this region (Raynolds and Johnson 2003; Hicks et al. 2002).

Study of the Ravenscrag Formation flora of the Big Muddy Valley, south-central Saskatchewan provides a link between the Canadian floras found in Alberta and Saskatchewan to the floras found to the south. The Big Muddy Valley is positioned to facilitate this link, because unlike the deposits found at Ravenscrag Butte, the Big Muddy Valley is part of the continuous Williston Basin/Powder Basin, a large depostitional basin that extends across North Dakota, South Dakota, Montana and Wyoming. Collections from the numerous fossiliferous beds of the Big Muddy Valley facilitate the compilation of a flora from the region, and facilitate this link.

The primary goal of the present project is to provide preliminary investigations into the many potential paleobotanical localities in the region and to collect representative floras from these localities, noting the similarities and differences

between the collections from the Big Muddy Valley and other Paleocene localities. The taxonomy of this study follows traditional methods, as compared to the morphotyping utilized in physiognomic studies (Johnson 2002). The goal of the taxonomic anaylses is to provide an appropriate name, noting specifically the confidence in the application of the name, as well as confidence in the accuracy of the taxonomic assesment. However, the goal of this study is to assess the material present in this study, and to only attempt to solve the recognized taxonomic difficulties when conclusive material is recovered. Limits to this endeavour are imposed by the quality and quantity of material recovered The collections from this study will provide a framework for future workers wishing to explore the numerous fossiliferous beds in the region, as well as provide a data point in the understanding of the greater regional context.

Organization of this thesis follows the conventions of a paleobotanical study in a geological context. Stratigraphy, although not truly a material, is placed between the materials and methods chapters. Additionally, rather than distinct chapters, the results are incorporated into the systematics, which also includes discussion in the form of remarks. Appendix A, a study into the taxonomy of *Glyptostrobus* is separated from the main body of text as it primarily utilizes materials found elsewhere in the Northern Hemisphere. However, its inclusion is justified, as resolution of that study is important to the understanding of the specimens of the Willow Bunch Lake map area.

CHAPTER 2
MATERIALS

Central to this project is a fossil flora collected from the Big Muddy Valley in the Willow Bunch Lake map area (72H) of Southern Saskatchewan. Hundreds of specimens have been collected, and currently exist in three separate collections. The first specimens were collected by J. F. Basinger and associates in 1992, from localities labelled US 927 to US 939 (formerly informally designated US92-2 to US92-16) in the University of Saskatchewan Paleobotanical Collection (USPC). Second, a large collection stored in Bengough, Saskatchewan was collected since the late 1990s by high school science teacher Mr. Adriel Larson. These were partially catalogued in 2005 by the present author. Finally, during the 2003 and 2004 field seasons, specimens were collected specifically to support the present project from localities throughout the valley (fig. 1 and table 1) (see appendix B for a detailed listing of the localities). A binomial, using a number and letter scheme of locality names was developed for the area. The numbers refer to "regions", introduced during the intial survey of the area; additional regions were later added to this framework. Nine regions are presently designated. Within each region, individual localities were asigned a letter name as they were encountered. Localities US 817 (1A), US 820 (1D), US 822 (2A), US 826 (2E), US 828 (3B), US 830 (3D), US 832 (4B), US 834 (5B), US 840 (7A), US 843 (9A) all have extensive collections. All regions except regions 4, 7 and 8 occurred close to the K-T boundary (approximately 65.5 million years ago). Regions 4, 7 and 8 occurred in zone P4 of Demchuck (approximately 58 million years ago) (Demchuck 1990). Other localities did not yield large collections, although they contributed important information to the flora. The majority of the localities also have an informal nickname, primarily assigned by Mr. Larson. These were maintained in the thesis to foster future communication and facilitate cross referencing between collections, as the number codes were alien to his system. The Royal Saskatchewan Museum (RSM) will curate the figured collections.

Impression and compression fossils dominate the collections. Some paper shales were collected, which appear to produce cuticles, although maceration for extraction and identification was beyond the scope of this project. Some petrified wood has been discovered in the area, but it is too crushed and deformed to be identifiable (A. Csank, personal communication 2004). In addition to the paleoflora, a small fauna has been recovered from the Big Muddy Valley, including crocodiles, champsosaurs, and at least two types of turtles and gars in the vertebrate fauna, and a number of gastropods and one bivalve in the invertebrate fauna. These specimens contribute to our understanding of the climate and environmental setting. Besides the fossil materials recovered from the Big Muddy Valley listed here, additional specimens (Appendix A) were utilized in an integrated study of *Glyptostrobus* within the Paleogene.

Locality	Nickname	Latitude	Longitude
US 817	1A Gopher Hole	49° 14.006'N	105° 09.680'W
US 818	1B Easy Chair	49° 14.181'N	105° 09.520'W
US 819	1C Gate Site	49° 14.222'N	105° 09.768'W
US 820	1D TP site	49° 14.112'N	105° 09.583'W
US 821	1E	49° 13.531'N	105° 10.615'W
US 822	2A Eagle's Nest	49° 15.704'N	105° 08.483'W
US 823	2B Dino Footprint	49° 15.588'N	105° 09.143'W
US 824	2C Stump site	49° 15.588'N	105° 09.143'W
US 825	2D	49° 15.359'N	105° 09.032'W
US 826	2E Dino Footprint upper	49° 15.588'N	105° 09.143'W
US 827	3A Bull Snake site	49° 14.593'N	105° 05.939'W
US 828	3B Skinny Leaf site	49° 14.455'N	105° 05.961'W
US 829	3C Upper Hesjedal	49° 14.455'N	105° 05.961'W
US 830	3D	49° 14.903'N	105° 05.723'W
US 831	4A RCMP	49° 01.713'N	104° 52.570'W
US 832	4B Buff Facies	49° 02.172'N	104° 49.138'W
US 845	4C Shot At	Unknown	Unknown
US 833	5A Lower Paradis	49° 13.110'N	105° 13.994'W
US 834	5B Upper Paradis	49° 13.013'N	105° 14.051'W
US 835	5C Too Hot	49° 13.785'N	105° 14.288'W
US 836	5D	49° 13.343'N	105° 14.363'W
US 837	5E Big Point	49° 14.921'N	105° 12.942'W
US 838	6A Ivan's Section	49° 14.383'N	105° 07.855'W
US 839	6B Ivan's Site	49° 14.383'N	105° 07.855'W
US 840	7A Foley's	49° 15.793'N	105° 27.271'W
US 841	7B Fullies	49° 15.845'N	105° 27.556'W
US 842	8A Mine Site	49° 16.057'N	105° 29.369'W
US 843	9A McCuaig	49° 13.005'N	105° 02.275'W
US 844	9B	49° 13.005'N	105° 02.275'W

Table 1: Locality information. More information on all of these localities is found in appendix B. Locality US845 is found south of Big Muddy Lake, but the latitude and longitude are unknown, as it was visited by Mr. Larson alone.

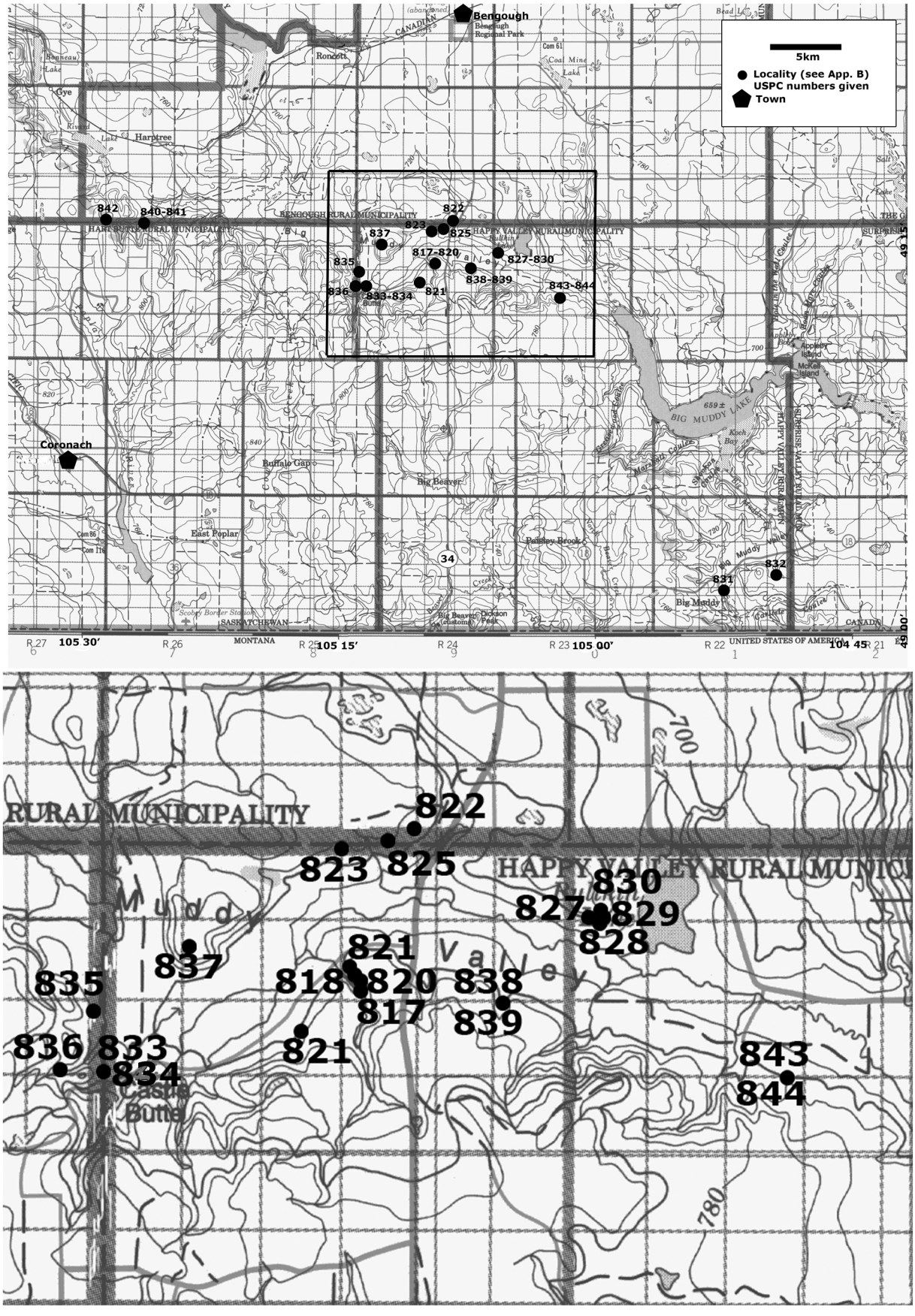


Figure 1: Localities utilized in this study.

CHAPTER 3
STRATIGRAPHY

3.1 The Ravenscrag Formation

Stratigraphically, the flora featured in this study was recovered from the Ravenscrag Formation. The Ravenscrag Formation consists of all beds of Paleocene age in southern Saskatchewan and adjacent southeastern Alberta (Dawson et al. 1994). It lies conformably or nearly conformably on the Frenchman Formation, which is latest Maastrichtian in age. It is overlain unconformably in parts by the Eocene-Oligocene Cypress Hills Formation and in other parts by layers of Quaternary sands, gravels or till. The type locality for this formation is Ravenscrag Butte, found in the Cypress Lake map area (Fraser et al. 1935; Furnival 1946; McIver and Basinger 1993).

The contact of the Ravenscrag Formation and underlying Frenchman Formation is designated as the K-T boundary (Furnival 1946). There are no mineralogical differences between the two formations in southern Saskatchewan, resulting in misidentification of these two formations as continuous Ravenscrag Formation (Fraser et al. 1935). The boundary has been delineated by a number of factors, which may or may not be present in any specific area. The four most common traits are as follows.

First, *Triceratops* sp. (and other dinosaurs) remains are found only in the Frenchman Formation. Their presence resulted in the nickname "*Triceratops* beds" of the Ravenscrag Formation in early reports (Fraser et al. 1935). Dinosaur remains were the earliest recognized indicator to distinguish between the two formations. However, faunal remains, in particular large animals, are rarely preserved, especially in the lowland swamp environments of the Ravenscrag Formation, making it a poor indicator in the majority of localities.

Second, the Frenchman Formation is not typically coaliferous. The Ravenscrag Formation (*sensu stricto*) was originally called "the coaliferous unit of the Ravenscrag Formation" (Fraser et al. 1935; Furnival 1946). The non-coaliferous portions of the initial description became the Frenchman Formation in later revisions. The Ravenscrag

Formation contains nearly all of the coal-bearing strata, although there are thin coals below the Ravenscrag Formation in places. It is common for the lowest coal in the section (especially the first major coal layer) to be used as a proxy for the base of the Ravenscrag Formation. In the Willow Bunch Lake map area, a distinctive set of three coals occurs at the base of the Ravenscrag Formation, facilitating rapid stratigraphic positioning during field studies (A.R. Sweet, Big Muddy Section GSC 5-27-3-24 W2).

Third, in some areas a distinctive K-T boundary clay is present (Lerbekmo et al. 1999). This thin, iridium-rich clay layer (< 10 cm), noted as diagnostic of the boundary by Alvarez et al. (1980), is missing from many areas, including the Willow Bunch Lake map area featured in the present study (72H).

Fourth, palynology can be used to determine the boundary, as there are regionally distinctive marker species present both in sections preserving a distinct boundary and more distant localities such as the Big Muddy Valley. Palynology is currently considered the most accurate method for determining the stratigraphic position of the K-T boundary in the region. Pollen zones for the Cretaceous and Paleocene were developed for the Western Interior (Demchuck 1990; Kroeger and Steadman 1990; Braman and Sweet 1999), based primarily on two genera: *Aquiliipollenites* and *Wodehousia*. Species of these palynomorphs are used to define the palynozones for the latest Cretaceous and Early Tertiary in the Western Interior basins of North America. This palynological framework is the primary method of determining the K-T boundary in the region, and was used to identify the triple coals mentioned above as the base of the Ravenscrag Formation in the Big Muddy Valley.

There are several sub-units of the Ravenscrag Formation. In the type section there are two distinct facies, designated the grey facies and the buff facies (Furnival 1946). Both of these facies consist of similar mixed sands and fine-grained sediments, typical of meandering river floodplain deposits. The grey facies is basal, encompassing the Early Paleocene. The buff facies is considered to be Middle Paleocene age in the type area and the Wood Mountain bore hole (Braman and Sweet 1999). However, the buff facies seems to extend into the Late Paleocene farther east in the province. A change in sediment source throughout most of the province was likely responsible (Catuneanu and Sweet 1999; Fraser et al. 1935). It is also be common to observe at least

one facies reversal in the section. The most important stratigraphic indicators in each of the map areas in the south of the province are the coal zones. In each map area, there are a number of large, distinct coal zones with numerous thin coal layers throughout the rest of the section, each with a specific name (Whitaker 1978).

The colour shift from grey to buff is regarded as a potential climate change (Fraser et al. 1935; Furnival 1946; McIver and Basinger 1993). The current explanation interprets the buff facies as reflecting a minor phase to drier conditions (i.e. oxidizing) throughout the Middle Paleocene. The grey colour is thought to represent anoxic conditions, as the iron content of water is reduced (Fe^{2+}), causing green-grey staining of the fine sediments. Stagnant and nearly stagnant water bodies, which are common in coal swamps, tend to be dysaerobic or anoxic. Therefore, the two-tone facies of the Ravenscrag may reflect a change in the climate (i.e. wetter to drier) and source material. This interpretation may be extrapolated across the larger region as these rocks are roughly contemporaneous across the extent of the Ravenscrag Formation.

Unfortunately the buff facies lacks well defined stratigraphic markers, so the time of its initial appearance is unclear; it is also unclear whether the buff facies development was time-transgressive across the map areas. The buff facies is poorly constrained by the absence of palynomorph assemblages in the type locality and the Wood Mountain map area (Braman and Sweet 1999). Only a crude correlation with the regionally adjacent sediments is possible. The grey facies formed during the well-defined Early Paleocene, while the buff facies dates from the Middle Paleocene. Additional evidence indicating a Middle Paleocene age for these sediments includes paleomagnetism, sequence stratigraphy, and invertebrate biostratigraphy (Catuneanu et al. 2000). In the present study area, the buff facies has been designated as representing the Middle to Late Paleocene, based on palynofloras collected and analyzed from localities US 832, US 840 and US 841(Sweet 2007).

Geographically, the Ravenscrag Formation is found in many small basinal offshoots in the western portion of its distribution, including the eastern Alberta deposits and the deposits of the Cypress Lake map area. The deposits in Wood Mountain, Willow Bunch Lake and Estevan map areas represent the northernmost edge of the contiguous Williston Basin. Paleocene beds are delineated as the Fort Union Formation

in the American portion of the Williston Basin. Outcrops of the Ravenscrag Formation are most common in the west of the province, in particular in the Cypress Hills area, which has the most relief. Accessibility to outcrop is limited in most areas, as the majority of the formation is buried. Only in areas of glacial-formed relief and fluvial incision are natural exposures found.

3.2 Stratigraphy of the Present Study

The plant fossil localities established in the present study (Table 1), scattered along the Big Muddy Valley in southern Saskatchewan, represent a range of ages within the Ravenscrag Formation. Numerous localities were established from the extensive exposures along both sdes of the valley in this area. The majority of these localities, found near Highway 34, represent the basal part of the Ravenscrag Formation. Today, the base of the Ravenscrag Formation in the Big Muddy Valley lies at ~680m above sea level. This investigation focused on these newly measured sections, not the localities previously reported in the Willow Bunch Lake map area. The sections are of earliest Paleocene age, and the coal beds previously used as a proxy for the K-T boundary are identifiable in most outcrops. The valley floor dips in elevation to the southeast, towards Big Muddy Lake, located to the east of Highway 34; in contrast, the tops of the valley walls are not inclined. Farther away from the lake, in the valley, the sediments of interest are higher in the section. The K-T boundary is not present in the exposures by Castle Butte, which is 18 km west of Highway 34 whereas the beds that represent the K-T boundary age are present in sections adjacent to Highway 34 and occur approximately 8.5m above the valley floor.

In addition to these basal sediments, three collections were made of putative buff facies. These strata were difficult to correlate to the basal Paleocene buff sediments adjacent to Highway 34. Sediments were collected south of the lake and lie high in the section, likely above the Willow Bunch coal zone. Another collection was also recovered from the Poplar River mine. This small collection was gathered from overburden above the Hart coal zone. A third collection was made of sediments above the Hart coal zone, likely at or above the level of the Willow Bunch coal zone (Sweet 2007). These localities of the third collection are not in the Big Muddy Valley, but in

some nearby uplands adjacent and above the current mine location, at a level > 800 m above current sea level (Broughton 1978; personal measurement 2003). This interpretation also agrees with the palynostratigraphy determined by Sweet (2007).

Outcrops in the Willow Bunch Lake map area also expose early Late Cretaceous sedimentary rocks, consisting of the Eastend Formation, Whitemud Formation and Frenchman Formation, and these extend upwards to the Late Paleocene Ravenscrag Formation (Braman and Sweet 1999; Sweet 2007). In the Big Muddy Valley, all of these formations except the Eastend Formation are present in outcrop (Catuneanu and Sweet 1999). There are many depositional hieatuses within the represented formations that contribute to the section in the Willow Bunch Lake map area, notably the one at the K-T boundary. This differs from the Ravenscrag Formation type-section, which represents continuous sedimentation across the boundary (Broughton 1978).

The most important stratigraphic indicators in each of the map areas in the south of the province are the coal zones. In each map area, there are a number of thick, distinct coal zones, each with a specific name, with numerous thinner coal layers throughout the rest of the succession (Whitaker 1978). In the Willow Bunch Lake map area, the Landscape coal zone near the base of the Ravenscrag Formation is the oldest major coal zone in the area. Despite being low in section, this unit does not correlate with the Furnival coal zone of the Cypress Lake map region (Broughton 1978). The Landscape coal zone is overlain by the Fife Lake coal zone, followed in turn by the Hart coal zone (the most economically utilized of these zones), the Coronach coal zone and, finally, the Willow Bunch coal zone (Broughton 1978). Shaft mining at the turn of the 20th century focused on coal members of the Landscape, Hart and Willow Bunch zones (Broughton 1978). Current strip mining utilizes the Hart and Willow Bunch zones.

The stratigraphy of the map area is difficult to discern due to the uniform mineralogy and few stratigraphically significant marker beds. A few markers, however, are available to establish gross correlation. Lithology can be used to differentiate the Whitemud from the Frenchman and Ravenscrag Formations. Additionally, the grey facies are notably distinct from the buff facies within the Ravenscrag Formation (Fraser et al. 1935). The K-T boundary, often designated by the first major coal layer in the area, is commonly a 1 m-thick coal composed of three distinct beds (GSC Big Muddy

Section 5-27-3-24 W2). However, confident designation of this coal typically requires the Whitemud Formation to be present in the same exposure, otherwise it can be difficult to distinguish these diagnostic beds, as both the Frenchman Formation and Ravenscrag Formation are consistent in lithology and mineralogically. When the thick coal zones are identifiable, it is easier to identify stratigraphic position in a section. While these are the most useful markers for field correlation within the Ravenscrag Formation, they are often missing from section. Additionally, it can be unclear which coal is being observed in new areas of study. The most accurate method of correlation both within and beyond the map area is palynology; however, this is a time consuming technique that requires specific expertise.

The Willow Bunch coal seam has been identified as Middle Paleocene, within the *Aquillapollenites spinulosus* zone of Demchuck (Demchuck 1990; Sweet 1993; Sweet 2007). The youngest verified beds of this area show that the strata extend into the Late Paleocene *Caryapollenites wodehousei* assemblage of Demchuck (1990), with palynomorphs approaching the *C. veripites* morphology, which suggests a younger portion within the *C. wodehousei* assemblage. This age was obtained at locality US 832, but this locality is only half way up the exposure, so there are younger beds in the map area, although how much younger is unclear. It is expected that all of these beds are still of Paleocene age, as there have been no reports from Saskatchewan of the earliest Eocene palynomorph flora from Saskatchewan (A.R. Sweet, personal communication 2007).

The landscape of the Willow Bunch Lake map area contains few deposits that date from the period between termination of the deposition of Ravenscrag Formation and the glacial till that covers most of the area (Fraser et al. 1935). There are rare deposits of Oligocene age of limited extent, but these occur away from the localities examined in this study. The lack of post-Paleocene strata can be attributed to many factors. First, deposition was greatly reduced when the Western Interior underwent massive drying as the Cannonball Sea fully retreated and the Western Cordillera underwent additional uplift. This was further compounded by the overall global marine regression and drying trend due to the polar glaciation that has occurred since the beginning of the Oligocene.

There likely was some additional deposition in the region, but shield glaciation scoured the region during the Pleistocene glacial advances. It has been suggested that extensive sediments were deposited throughout the interior, and that the cessation of regional uplift and glaciation might have eliminated up to 3 km of sediment from the region (Dawson et al. 1994). These events also caused the current landscape development, with glacial meltwater erosion cutting the channels that produced the present outcrops. In particular, the Willow Bunch Lake /Big Muddy Valley-Lake complex formed as a local glacial run off channel. The coulee system present around US 840 is also glacial in origin, although not as obvious in origin as the main valleys and lakes. Given the widespread presence of till across the area, the entirety of the Willow Bunch Lake map area was likely glaciated in the Pleistocene (Parizek 1964). However, the meltwater channels carried away specific portions of the till.

3.3 Basinal Structure

Within the Willow Bunch Lake map area (72H), Late Cretaceous and Early Tertiary sediments are 30 m to over 100 m thick, and are exposed in many localities in the region, primarily along the walls of the Big Muddy Valley and the two adjacent lakes, Willow Bunch Lake and Big Muddy Lake. The inclination of the beds was probably horizontal during those times, with no record of regional tectonic activity visible in the outcrops (Braman et al. 1999). Additionally, deposition occurred during times of relative regression of the Cannonball Sea, which was then present towards the east (Catuneanu and Sweet 1999). One explanation for the formation of these sediments is the deep erosion and collapse of the Prairie Evaporite in two regional troughs: the Hummingbird and Coronach troughs (Broughton 1977). This scenario may also account for the formation of the Williston Basin proper. Evidence supporting this model includes: 1. Reduced thickness of Prairie Evaporite strata in these regions; 2. The discontinuity between the clearly terrestrial sediments, flora and fauna, and the marine affinity for some minerals present that could represtnt the influence of upwelled brine from dissolved evaporites (Potter et al. 1991); 3. Structural analyses have confirmed the existence of the Coronach and Hummingbird Troughs mentioned above (Broughton 1977). These two trenches formed by the collapse of the Prairie Evaporite in the region

surrounding the study area, with the Hummingbird Trough to the east and the Coronach Trough to the west. The Big Muddy Valley lies in the depositional ridge between these two troughs, with the outlying localities of this study (region 7, region 8, region 4) perhaps intersecting the slopes of the troughs. Coal mines in the region exploit the thicker sediment accumulation in this intersection.

The sediment source was from the northwest in the emerging Rocky Mountains of northern Alberta. This is different from the Fort Union localities to the south, which derived sediment from lateral sources (Broughton 1978). Variations in mineralogy indicate the sediment in the Big Muddy Valley traveled through many similarly-aged localities across Alberta and Saskatchewan (Potter et al. 1991).

Sediments in the numerous basins of the Western Interior originate from the Cordillera, which was undergoing uplift at that time. The Williston Basin incorporated sediments from numerous areas to the west (Broughton 1978; Daly et al. 1990; Potter et al. 1991; Diemer and Belt 1991; Johnson and Ellis 2002). For periods during the Cretaceous, the sea covered most of the basinal area (Catuneanu and Sweet 1999; Lund et al. 2002). However, by the latest Cretaceous, the sea had retreated to the south and east, so the sediments were terrestrial (Dawson et al. 1994). During the Paleocene a slight transgression of the Cannonball Sea occurred, but in the area where sediments of the Ravenscrag Formation were depositied, conditions were not marine. The Cannonball Sea retreated steadily after this time. It has been estimated that up to 3 km of sediments were eroded from the region through rebound after the Laramide orogeny and later glaciation (Dawson et al. 1994). This led to limited preservation of the Tertiary deposits.

3.4 Regional Stratigraphy

The mid-continent of North America has numerous formations of comparable age to the Ravenscrag Formation. Other formations of this age recognized in Alberta include the Paskapoo Formation, Porcupine Hills Formation, Coalspur Formation, Willow Creek Formation and Scollard Formation (Chandrasekharam 1974; Christophel 1976; Dawson et al. 1994; Hoffman and Stockey 1999). To the east of Saskatchewan, the Turtle Mountain Formation occurs in western Manitoba. In the Unites States portion

of the Williston Basin, the beds compose the Fort Union Group, which has numerous local names in various states (Hickey 1977; Catuneanu and Sweet 1999). It is difficult to correlate between these formations. Palynology and magnetostratigraphy are used to provide correlations, as these sedimentary sequences contain few macrofossils (Hartman and Kihm 1990; Lerbekmo 1985; Lerbekmo 1999; Nambudiri 1987; Sweet 1978; Sweet and Braman 2001); however, there are intra-regional variations in the palynological and magnetostratigraphic records, especially in the chrons preserved in the various localities.

Across the Ravenscrag Formation, the coal zones can be used for broad correlation, for in each area there are a number of basal coals. As already noted, there are regional names for these coals, such as the Landscape coal zone, used in the Willow Bunch Lake map area. The middle coal zones, represented by the Fife Lake, Hart and Coronach zones of the Willow Bunch Lake map area are restricted to those areas adjacent to the Wood Mountain map area. These are higher in section than those in the Cypress Lake map area but were not deposited in the Estevan area. It has been proposed that the Willow Bunch coal zone correlates with the Estevan zone in the east (Sweet 1978) and the Lebo Formation to the south in Montana, the Slope Formation in the Dakotas, and with the Paskapoo Formation to the west in Alberta (Catuneanu and Sweet 1999).

There are many formational names for similar beds of Early to Middle Paleocene age deposited in the basins of the Western Interior and parts of the Rocky Mountains. As mentioned above, the Ravenscrag Formation represents rocks of southern Saskatchewan and the connected basins of adjacent Alberta. The Ravenscrag Formation in the Cypress Lake map area represents the lowest Paleocene to early Middle Paleocene (Catuneanu and Sweet 1999). The Ravenscrag Formation preserved in the eastern half of Saskatchewan is the northernmost part of the continuous Williston/Powder Basin. The Ravenscrag Formation is entirely composed of terrestrial deposits.

The Turtle Mountain Formation represents the limited and localized Paleocene deposits in Manitoba. This formation extends from latest Cretaceous time through much of the Early Paleocene. It consists of terrestrial sediments, mostly termed the Goodlands Member, and marine sediments, termed the Peace Garden Member.

Alberta has many sedimentary basins, most related to portions of the Cordillera uplift, each of which has its own stratigraphic nomenclature. In the south, the Willow Creek Formation consists of latest Cretaceous and lower Paleocene deposits, and the Scollard Formation of the northern Alberta Basin spans the same time period. In the Foothills region the Coalspur Formation is considered to have the same stratigraphic range as the Scollard Formation and Willow Creek Formation. The middle Paleocene in the south is termed the Porcupine Hills Formation, which is thought to be comparable in age to the buff facies of the Ravenscrag Formation. In the north of Alberta, the Paskapoo Formation is of middle Paleocene age but it includes younger Middle Paleocene rocks than the type section of the Ravenscag Formation or Porcupine Hills Formation. Preservation of Paleocene materials across Alberta is confined primarily to a series of basins along the Rocky Mountains, particularly the Alberta Basin, Red Deer Basin and various small areas along the edge of the mountains. All latest Cretaceous and Paleocene formations in Alberta are terrestrial. Much like the sediments of Ravenscrag Formation, these sediments are largely undifferentiated terrestrial deposits, although being closer to the Rocky Mountains they include coarse sandstones and conglomerates. Variations in the amount and loction of uplift resulted in depositional diversity across the different regions, justifying local nomenclature (Dawson et al. 1994).

The Williston/Powder Basin is the main depositional system of the Great Plains of western North America since the Cretaceous (fig. 2). Paleocene rocks are included in the Fort Union Group. In North Dakota, the Ludlow Formation is an Early Paleocene terrestrial deposit and the Tongue River Formation is the equivalent Middle Paleocene terrestrial deposit. The marine sediments of the Cannonball Seaway inter-tongue with both of these formations representing the late Early and Middle Paleocene. In Montana, the Lebo Formation is Lower Paleocene, and the Tullock Formation which is Middle Paleocene. Montana lacks marine sediments of Paleocene age, similar to Saskatchewan and Alberta. Figure 3 summarizes the correlation between these formations.

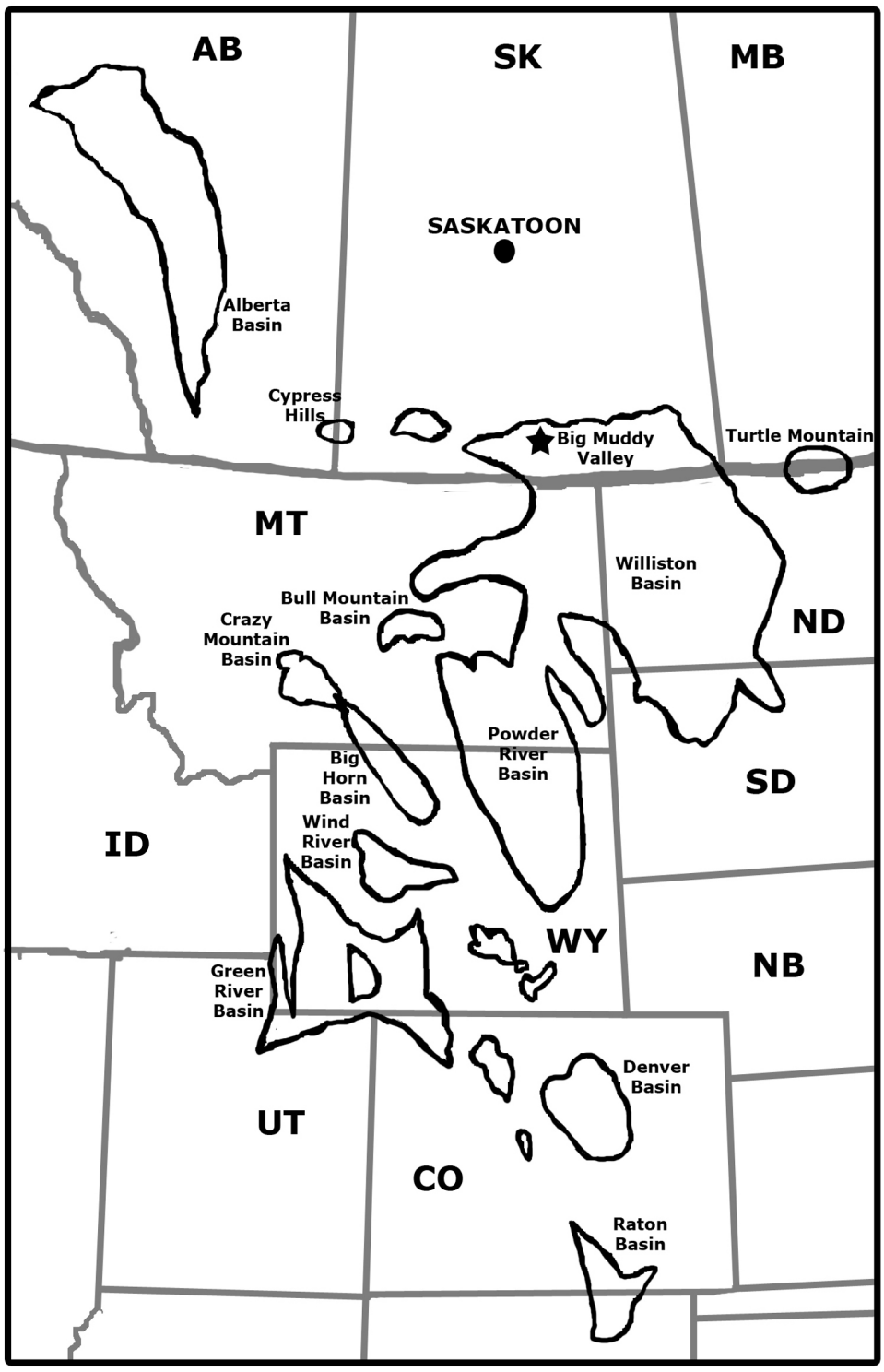


Figure 2. Paleocene Basins of the Western Interior. Modified from Dawson et al. (1994); Lund et al. (2002); Barclay et al. (2003).

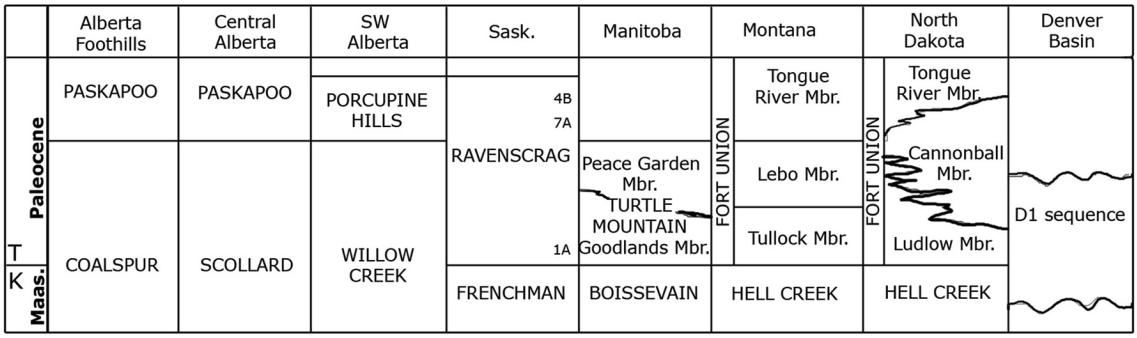


Figure 3. Correlation between Paleocene formations of the Western Interior. Adapted from Cantuneanu and Sweet (1999), Johnson (2002) and Barclay et al. (2003).

CHAPTER 4
METHODS

Fossils were collected with a sampling bias to maximize taxonomic diversity in a minimal number of specimens to minimize weight for transport over long field distances. No census data were collected or attempted at the localities. Sections were measured with 1.5 m walking sticks, marked at 10 cm intervals. Minimal natural erosion hampered strike and dip measurements; however, exposed beds indicated a predominance of original horizontality.

Traditional techniques were deemed appropriate for physical preparation and study of the fossils, in paricular microneedle degagement (Fairon-Demaret et al. 1999), and photography. Photography was primarily conducted with a Nikon D70 camera with an AF micro Nikkor 60mm 1:2.8D macro lens mounted on a copy stand. Additionally, some photos were taken with the same camera body mounted on a compound scope. Processing of the digital photographs was undertaken in Photoshop CS, mainly involving cropping and increasing contrast, both techniques utilized extensively in darkroom processing in traditional photography. Digital camera lucida was also performed using Photoshop CS and a 6x8 Wacom Intuos 2 tablet. These drawings facilitated study of leaf venation details in a similar fashion to traditional camera lucida techniques.

Nearest Living Relative (NLR) (Mosbrugger 1999) and Climate Leaf Analysis Multivariate Programmes (CLAMP) (Wolfe 1999) analyses were applied in an attempt to enrich our understanding of the Williston Basin palaeoclimate. Unfortunately,

CLAMP proved nonconducive, as the sites are dominated by non-CLAMP-able materials such as conifers, pteridophytes and herbaceous monocots (Wolfe 1999). Conversely, while NLR analysis was possible, it has been criticized, particularly by those who use CLAMP, to be inadequate, especially for this age of flora (Wolfe 1999). These workers challenge that the technique is limited by the absence of extant angiosperm genera in the Paleocene, although they concede that certain conifer and pteridophyte genera have remained unchanged since Palaeogene times (Mosbrugger 1999).

In addition to the listed methods, additional techniques were utilized in the study of *Glyptostrobus*, and are reviewed as an appendix, as that study was included in this thesis as a separate study in the form of another paper. Understanding the *Glyptostrobus* dominated environments of the Big Muddy Valley was enhanced by inclusion of materials from other localities.

CHAPTER 5
SYSTEMATICS

The systematics of Paleocene floras is currently in a state of major transition. This is brought on by many factors: first, paleoclimatic interpretations employ a modified system of taxonomy that utilizes individual organs as separate taxa; moreover, these taxa are rarely formally described, and do not look to revise the circumscription of the taxa; second, a shift in the interpretation of fossil angiosperm taxa has led to the change of the genera of many of the formally described taxa, as traditionally most of the taxa of Paleocene angiosperms have been included in modern genera. There is a trend to recognize substantial evolution since the Paleocene and that many cases of similarities in angiosperm leaf venation represent convergence; additionally, paleobotanical work in Siberia has become more thoroughly established in the literature. These taxa typically use Soviet nomenclature, which requires careful consideration for determining priority, of parallel systematics for many taxa. Besides these three recent trends, higher level taxa have been revised heavily due to the advent of molecular systematics (APG-II 2003). Therefore, nearly all biological taxonomy, especially for angiosperms, is undergoing major revisions at the present time.

Where applicable, this report will use the most recent taxonomic interpretations, with recognition that the taxonomy of these plants is in transition. Unfortunately the fossils utilized in this study were too fragmentary and poorly preserved to offer much in the way of taxonomic resolution. The fossils studied here are catalogued as a representation of floral diversity; hopefully serving as a baseline for future studies to consider in greater detail, and potentially for use in taxonomic revisions when preservation details permit. As a survey, the goal should not look to resolve all of the taxonomic issues, but rather to identify plants with appropriate commentarty to provide data for future studies seeking to resolve the issues.

Only vascular plants were recovered in the floral survey conducted in this study. Other surveys commonly recover rare non-tracheophyte elements, such as moss

gametophytes or fungal hyphae. The absence of the non-vascular plants likely reflects taphonomic limits and collector's bias rather than their absence in the paleoflora.

Descriptions of the angiosperm foliage follow the order and terminology utilized in the Manual of Leaf Architecture (Leaf Architecture Working Group 1999). This differs slightly from other systems, but increases correspondance with other recent paleobotanical studies.

Class Lycopsida
Order Isoetales
Family Isoetaceae Reichenbach
Genus: *Isoetites* Muenster
Species: *Isoetites horridus* (Dawson) Brown
Plate 1 fig. 1
Synonyms and References:
Carpolithes horridus Dawson, 1883, p. 21, pl. 1, figs. 3, 3a, 3b.
Antholithes horridus (Dawson) Dawson, 1887, p. 7.
Isoetites horridus (Dawson) Brown, 1939, p. 268, figs. 3, 6; Brown, 1962, p. 46, pl. 9, figs. 4, 8.
Localities: US 817
Figured specimen: US817-9008
Description: Partial rosette of small, linear leaves, 2-5 mm wide, over 17 mm long. All recovered specimens are incomplete. Fine marginal dentition. No venation, although one leaf exhibits some box-like structures, typically interpreted as collapsed air chambers.

Remarks: Only two specimens were recovered in the study area, both from locality US 817. These specimens are largely incomplete, each consisting of impressions of fragments of many adjacent linear leaves. These fragments are arranged in an arc, and on one of the two specimens, part of a corm appears to be present. These specimens are placed in *Isoetites horridus* due to the presence of air chambers and a putative corm. However, these traits are somewhat suspect, and better specimens are necessary for

proper diagnosis. This plant is always a rare element in similarly-aged paleofloras, and is often absent. More complete specimens from other localities clearly show a morphological arrangement of numerous linear leaves growing from a central corm (Brown 1962; Hickey 1977).

In the his original diagnosis of *Isoetites horridus*, Brown (1939) noted smooth leaf margins as a trait distinguishing it from *Isoetites serratus* Brown (1939), a species known only from the Cretaceous. However, Brown (1962) revised this stance with illustrated specimens of serate margined *Isoetites horridus* from the Paleocene. Therefore, the presence of fine serrations along the margins of the leaves in the present collection is not sufficient reason to assign them to another species, nor to extend the range of *I. serratus* into the Paleocene.

More complete specimens have been discovered in other localities across the Western Interior of North America. Affinities of these fossils to *Isoetes* L. are drawn from similar remains in other localities where sporangia have been found, such as specimens from Ravenscrag Butte (McIver and Basinger 1993). However, the specimens collected from the Big Muddy Valley do not have these diagnostic characters. Although the fragmentary nature of these specimens, combined with poor preservation, makes identification difficult, in measurement and ornamentation the Big Muddy specimens resemble *I. horridus,* illustrated by Brown (1962) and Hickey (1977). Unfortunately, except for one small fragment, the specimens from the Big Muddy Valley do not exhibit the box-like depressed air chambers present in both these leaves. However, the *Xantholithes propheticus* Ward specimens in Berry (1935) resemble *I. horridus* and have 2 distinct sections: the long basal portion of the appendages, which often do not show the air chambers (pl. XX Fig 1 Berry 1935), exhibit the marginal teeth, and include a distal tip, which is broader and clearly shows the air bladders.

McIver and Basinger (1993) and Hickey (1977) both found the spores of this plant appear similar, if not identical, to the extant genus *Isoetes*. However, the laminated leaves and spatulate tips of *Isoetites horridus* are unknown in *Isoetes*, which led both to assign the leaves to this extinct genus. This establishes a clear familial link between these two genera which clearly reside in the Isoetaceae.

Class Sphenopsida

Order Equisetales

Family Equisetaceae Michaux ex DeCandolle

Genus: *Equisetum* L.

Species: Unknown

Plate 1 fig. 2

Localities: US 842, US 820, US 822, US 831, US 834

Figured specimen: US842-9009

Description: Largest (primary?) shoots 2-3.5 mm wide, Internodes over 20 mm long. Leaves arising in whorls, 6.5-8 mm long. Lateral branches 1mm wide, arising from distinct nodes, also bearing whorled leaves. No strobili recovered, and none of the axes have the appearance of typical *Equisetum* fertile axes.

Remarks: This plant is a rare element of many of the localities in the present study, with the most readily identifiable and complete specimens recovered from localities US 842 and to a lesser extent US 820 and US 836. Generic assignment is possible due to the distinct architecture of the remains, which exhibit nodal whorls of leaves, branches and tubers, along with the distinct ridges in the internodal area. These are clearly sphenopsid traits and *Equisetum* is the only sphenopsid genus recognized from the Paleocene. Specific assignment was not attempted for these remains, as none of the traits preserved is diagnostic at the species level. There are many species of Paleocene *Equisetum*, many of which are ambiguous and the taxonomy is in need of revision, which will require clear and diagnostic materials. More complete and diagnostic remains were collected from Ravenscrag Butte and named *E. fluvatoides* McIver and Basinger (1989). The specimens from the Big Muddy Valley fall within the range of that species; however, they also fall within the range of other species of *Equisetum*. Some workers (Bell 1949; Christophel 1976) consider all Paleocene *Equisetum* to be part of the *Equisetum arcticum* Heer complex. This is a reasonable assessment, as there are likely many similar species of *Equisetum* that cannot be distinguished from each other with use of the dispersed remains.

Equisetum is a member of many Cretaceous and Tertiary paleofloras. It seems to have limited taphonomic distribution, as it preferentially grows in monotypic beds, often on sandy substrates (Hoffman 2002). *Equisetum*-bearing sandstones of the proper sort appear in almost every fossiliferous study area. Additionally, *Equisetum* has decay-resistant stems, so transported specimens can be found mixed in with other portions of a flora. Its unique morphology makes *Equisetum* readily identifiable within floras, although it is usually difficult to distinguish species.

Class Filicopsida
Order Filicales
Family Blechnaceae Presl.
Genus: *Woodwardia* J.E. Smith
Species: cf. *Woodwardia gravida* Hickey
Plate 1 fig. 3
Synonyms and References:
Woodwardia gravida Hickey, 1977, p. 109, pl. 4, figs. 7(7-11. pl. 5, figs. 1-2); McIver and Basinger, 1993, p. 21 pl. 7 figs. 2-3 (1-4,) (pl. 8, figs. 1-2).
Localities: US 820, US 822
Figured specimen: US820-9010
Description: Only sterile pinnae have been found in the study. The pinnae appear once pinnatifid. Pinnules, 10 mm long, 5 mm wide, adnate bases, acute rounded tips, offset origination. Non-anastomosing (US 820) or anastamosing (US 822) venation, once or twice dichotomous veins arising from central rachis in each pinnule. Margin finely serrate where visible.

Remarks: This plant is a rare element in the Big Muddy Valley flora, found in one or possibly two localities. It is identifiable as *Woodwardia* by the slightly offset pinnules and finely serrate margins on specimens of this size. One of the specimens resembles other ferns, primarily sterile *Osmunda macrophylla* Heer. However, it is much smaller than typical of *O. macrophylla*. *Woodwardia gravida* specimens have been reported with a number of morphologies (Hickey 1977; McIver and Basinger 1993). Fragments

representing much of the sterile variation of this species have been found: a specimen from US 820 closely resembles Plate 4 fig.7 Hickey 1977, whereas specimens from US 822 more closely resemble pl. 7, fig.1-3 McIver and Basinger 1993. It has been noted that *W. gravida* specimens can often be confused with *Onoclea hesperia* specimens, due to similar anastamosing venation that is often present in both (McIver and Basinger 1993). This is especially true in studies where *Woodwardia* specimens are more common (K.B. Pigg, personal communication 2006). However, the specimens identified in this study represent a morphology of this taxon that is difficult to confuse with *Onoclea*.

Woodwardia is a common element of many Paleocene floras in the Western Interior. Reproductive materials are needed for definitive species assignment. Hickey (1977) notes other fossil *Woodwardia* spp. found at the same localities that resemble *W. gravida*, other than the continuous sporangia present along the rachis. Therefore, the Big Muddy Valley specimens are assigned to cf. *W. gravida*, because they lack sporangia. *Woodwardia* generally seems to be an element of swamp floras, although based on the growing habits of the extant relatives they likely grew as part of the understory of less inundated portions of the forest (Collinson 2001). It is unclear how large the fossil species grew, as only fragments of the fronds have been found, both in the Big Muddy Valley and other studies (Hickey 1977; McIver and Basinger 1993; Collinson 2001). However, extant species of *Woodwardia* are large ferns, with the largest specimens having fronds reaching 3 m in length (Pigg and Rothwell 2001).

Family Dryopteridaceae Herter

Genus: *Onoclea* L.

Species: *Onoclea hesperia* Brown

Plate 1 fig. 4

Synonyms and References:

Onoclea hesperia Brown, 1962, p. 43, pl. 7, figs. 1 and 4; McIver and Basinger, 1993, p. 21, pl. 6, figs. 3-7, and all synonymies listed.

Localities: US 822, US 830, 1992 collections

Figured specimen: US830-9011

Description: Fronds are bipinnate-pinnatifid; no complete fronds have been recovered from the area. Fragments are at least 18 mm wide, at least 31 mm long. The lobes arise at angles of 30 degrees. Each pinnule has a strong central vein, with extensive lateral anastamosing veins, which continue to the margins. The margins are entire.

Remarks: *Onoclea hesperia* Brown specimens are common in many localities in the area. It is the most common fern present in the US 830 collections, where it is amongst the most common plant overall, and is also common in the US 822 collections and collections taken from the area in 1992 (USPC 935, as well as other localities). This fern can be identified by its complete margins and anastamosing venation. It is most likely to be confused with *Woodwardia* spp., which also has anastamosing venation. However, *Woodwardia* spp. (particularly *W. gravida*) pinnules have open dichotomous branching away from the rachis, often have preserved serrate margins, and are generally smaller than *O. hesperia* specimens (McIver and Basinger 1993). Fertile axes, when recovered, for both plants do not resemble one another.

This fern is a common element of Paleogene localities of the Northern Hemisphere (Colinson 2001). Differing taxonomies have been proposed for this fern, which closely resembles *Onoclea sensibilis* L., the extant sensitive fern. The extant and the fossil materials share sufficient characters that some have suggested a unification of the taxa (Rothwell and Stockey 1991). However, the use of extant taxa for fossil forms has been discouraged, due to the difficulties associated with fragmentary materials and time differences. Two fossil species have been proposed for this material, *O. hesperia* Brown, and *O. herbridica* (Forbes) Gardner and Ettingshausen. These species are primarily distinguished on the basis of fertile fronds, which *O. herbridica* has and *O. hesperia* does not. Fertile fronds have not been found in the Big Muddy Valley, and are only rarely found elsewhere (Boulter and Kvacek 1989). Therefore, following the general precedent of McIver and Basinger (1993), who also did not recover fertile fronds, the specimens from the Big Muddy Valley have been placed in *O. hesperia*, until fertile remains are found to show clear affinities with one of the other species. Within the study area, locality US 830 produced the most and best preserved specimens, making it the most likely locality to find fertile remains in any future study.

Family Dennstaedtiaceae Pichi-Sermolli

Genus: *Dennstaedtia* Bernhardi

Species: *Dennstaedtia americana* Knowlton

Plate 2 figs. 1-2

Synonyms and References:

Dennstaedtia americana Knowlton, 1910, p. 492. pl 63, fig. 4, pl 64, figs. 3-5; Brown, 1962 p. 42, pl. 6, figs. 1,2, 5-7; McIver and Basinger, 1993, p. 19, pl. 5, figs. 2-4, and all synonymies listed.

Localities: US 817, US 832, US 834

Figured specimens: US832-9012, US832-9013

Description: Once pinnate pinnatifid fronds, thought to be twice pinnatifid otherwise, delicate. Sterile raches are over 25 mm long. The leaflets have entire margins, although irregularly shaped. Non-anastomosing veins with up to 8 dichotomising events 1mm – 2mm apart. Usually fewer dichotomies, varying throughout the blade due to slightly uneven branching leading to lobed leaflets, up to 20 mm long, 10 mm wide. Fertile raches are over 45 mm long. Pinnules are 3-9 mm long; veins with up to 6 dichotomies. Sporangia are at the ends of veins, in clusters due to close final dichotomies. Up to 4 clusters per leaflet.

Remarks: Sterile and reproductive pinnules have been recovered from locality US 832, while only sterile pinnules were recovered from US 817 and US 834. These specimens resemble what has been referred to as *Dennstaedtia americana* due to the terminal/marginal sporangia, closely resembling pl. 6 Fig 7 of Brown 1962. This species is understood to be doubly pinnate (McIver and Basinger 1993), with another order of rachis beyond what is seen in this collection. The lack of multiple levels of pinnatifid branching is due to poor preservation, and does not seem to represent a difference in species.

Boulter and Kvacek (1989) suggested that *Dennstaedtia blomstrandii* (Heer) Hollick was the correct name for this plant, arguing that *Dennstaedtia americana* was a junior synonym adopted because of a lack of reproductive materials at the type locality.

They felt that this deficiency was remedied through recently rediscovered plates made by Nathorst in the late 1800s, and united the two species. However, McIver and Basinger considered the evidence and found the two species were separate, rejecting the unification proposed by Boulter and Kvacek (1989). Hoffman (2002) agreed with the assessment of Boulter and Kvacek (1989) and opted to use *D. blomstrandii* for specimens from the Joffre Bridge.

In 1993, Kvacek and Manum proposed that *Dennstaedtia blomstrandii* should be *Coniopteris blomstrandii* (Heer) Kvacek and Manum due to the presence of smooth walled spores recovered from *in situ* sporangia in new specimens from Spitzbergen. They noted that extant *Dennstaedtia* does not have smooth walled spores and, in their opinion, this showed that the traditional placement of these specimens should be in Dicksoniaceae, not Dennstaedtiaceae. They followed the assessment that *D. americana* and *D. blomstrandii* were the same species, so they believed that this change applies to *D. americana* as well. Given that this synonymy is not universally accepted, Collinson (2001) has stated that a review of *D. americana* is needed, as no *in situ* spores have been analyzed yet to confirm familial and generic placement.

Family Azollaceae Wettst.
Genus: *Azolla* Lamarck
Species: *Azolla schopfii* Dijkstra
Plate 2 fig. 3-4
Synonyms and References:
Azolla schopfii Dijkstra 1961, p. 9; Sweet and Chandrasekharam, 1973, p. 1493, figs. 2-23, and all synonymies listed; McIver and Basinger, 1993, p. 22, pl. 8 figs. 3-6.
Localities: US 840
Figured specimens: US840-9014, US840-9015
Description: Plants likely floating aquatics. Alternate branching, branches arising every 4-6 mm along the main axes, growing more imbricate distally. Leaves alternate on stems, at least 3 ranks of branching. Leaves are 2- to 3-pinnate. Leaflets rounded, 1.5-3 mm long, 1 mm wide. Roots present in small bunches, at least 5 roots per node, all bunches arising on one side of a node, bundles 6 mm apart; roots at least 12 mm long.

Remarks: This species is found only in US 840, where it is the sole pteridophyte. These specimens are definitively identifiable due to the association of megaspores of *A. schopfii* (Sweet 2007) and macrofossils that resemble other finds of *A. schopfii* from this locality. The macrofossils exhibit the numerous bunched roots (pl. 2, fig. 4), branched stems that do not exhibit a planar orientation (pl. 2, fig. 3), and distinct round leaflets that match other descriptions of this species.

Azolla species identification is generally considered to require megaspores (Sweet and Chandrasekharam 1973; Hoffman and Stockey 1994; Collinson 2001). Of the fossil species, identification of *A. schopfii* is least reliant on association of megasopores and vegetative remains, as it retains more pleisiomorphic traits than other *Azolla* species. These traits include three dimensional branching instead of planar branching exhibited by other *Azolla* species, distinct and separate leaves, and well developed roots. Although not found in connection, the close association of the megaspores (Sweet 2007) and macrofossils makes identification quite solid, especially considering that these remains appear identical to *A. schopfii* remains from Ravenscrag Butte (McIver and Basinger 1993) and the Genesee localities (Sweet and Chandrasekharam 1973), both of which included *in situ* megaspores.

The distribution of this species in time and space is complicated by the need for both palynofloras and macrofloras at the same locality for confident identification. The specimens in the current study are found in white clay, and are likely *in situ*. However, it is found in sandier sediments at Ravenscrag Butte, and is commonly found in association with other elements, including *A. vellus* in one of the two localities it appears in at the Ravenscrag Butte (McIver and Basinger 1993). *Azolla* spp. are aquatic plants in all interpretations. Megaspores of another species of *Azolla* are also found in association with these remains in US 840, which is similar to the association of *A. schopfii* and *A. vellus* at US1 (McIver and Basinger 1993), perhaps indicating that it was common to find multiple species of *Azolla* in one locality.

Interestingly, *Azolla schopfii* appears relatively high in section throughout the Ravenscrag Formation with estimated ages of the localities always within the middle Paleocene (Sweet 1999; Sweet 2007), which runs somewhat counter to the

plesiomorphic character states exhibited by this species, as more derived species are found lower in section than these localities. This merely reflects that *A. schopfii* was somewhat of a relic species in the Paleocene, not that its traits are more highly derived as this might suggest, as studies into the genetics of the extant show that these traits are ancestral (Hoffman and Stockey 1994). *Azolla schopfii* has the most plesiomorphic traits of any known *Azolla* species, and has been used as a model for what the other early species would have looked like (Hoffman and Stockey 1994).

Genus: *Azolla* Lamark

Species: cf. *Azolla vellus* (Dijkstra) Jain and Hall

Plate 2 fig. 5

Synonyms and References:

Triletes vellus Dijkstra, 1961, p. 7, pl. 1, figs. 16-20.

Azolla vellus (Dijkstra) Jain and Hall, 1969, p. 524, figs. 1-6, 9, 11; McIver and Basinger, 1993, p. 23, pl. 9, figs. 1-7.

Localities: US 845

Figured specimen: US845-9016

Description: Floating aquatic. Pinnatifid leaves flattened into a plane. It is unclear as to number of orders, but at least once pinnatifid. Main rachis length over 12 mm long, with secondary rachillas arising every 1 mm. Secondary rachillas arise 50 degrees off main rachis direction. After every branching event, main rachis diverges 60 degrees in the other direction from the secondary segment, giving the main rachis a zig-zag appearance. Secondary rachillas up to 5 mm long. Leaflets lanceolate, appear only on secondary rachis. 0.5-1 mm long, 0.2 mm wide, 0.5 mm between leaflets on one side.

Remarks: This species is found only in locality US 845, where it is amongst the commonest elements. Only sterile sporophytes have been recovered, so it cannot be placed definitively in a species, as *Azolla* species designation typically requires megaspores (Sweet and Chandrasekharam 1973; Hoffman and Stockey 1994). This species of *Azolla* can be distinguished from *Azolla schopfii* by the compressed and flattened branching with distinct “zig-zag” central axis to each rachis, which closely

resembles *Azolla vellus* specimens reported from Ravenscrag Butte (McIver and Basinger 1993). However, other species of *Azolla*, such as *A. stanleyi* Jain and Hall have traits that resemble these as well (Hoffman and Stockey 1994). However, the forms of these traits exhibited by the specimens of the present study more closely resemble *A. vellus* and, therefore, have been placed in conformity with this species. The characters of this *Azolla* sp. are more derived than those of *A. schopfii*, and this plant more closely resembles the extant. However, it is less derived than any of the extant species, such as the fact that it exhibits central veins within the leaves.

There were no arboreal elements found in locality US 845. Instead, it consists entirely of arguably aquatic plants including *Paranymphaea crassifolia*, *Quereuxia angulata* and this species of *Azolla*. However, the aquatic status of *Paranymphaea* has been debated (McIver and Basinger 1993). This high aquatic content association is also present in Ravenscrag Butte, as the associated species listed by McIver and Basinger for *A. vellus* are largely the same plants as are present in this bed, with the addition of "*Trochodendroides speciosa*" (McIver and Basinger 1993). This aquatic flora is not the dominantly preserved flora, but it is common to isolated beds of this material within the greater swamp flora context. *Azolla* is typically found in calm water environments like deep lake sediments, and is often considered a paleoenvironmental indicator of this environment (Collinson 2001).

Family Schizaeaceae Kaulfuss
Genus: cf. *Lygodium* Swartz
Species: unknown
Plate 3 figs. 1-4
Localities: US 834
Figured specimens: US834-9017, US834-9018, US834-9019, US834-9020
Description: Specimens are heavily branched pinna fragments with elongate, open dichotomizing (non-anastomosing) veins. Veins dichotomize two to four times from rachis to margin. Pinnae are 20 mm wide, over 40 mm long, but part of a much larger plant. Leaves have compound serrate margins.

Remarks: Specimens are highly fragmentary. However, the venation, size and shape resemble specimens assigned to *Lygodium kaulfassi* Heer by Brown (1962) and Hickey (1977), although they differ in the presence of compound serrate margins. *Lygodium prestwichii* (Gardner and Ettingsh.) Gardner from clay beds in Europe is distinguished from *L. kaulfassi* by the presence of serate margins. However, there is some doubt as to the veracity of this claim, raised primarily due to the identification of *Eostangeria pseudopteris* Kvacek and Manchester 1999. This cycad is fernlike, and is said to be difficult to distinguish from ferns without cuticles. It has serrate margins and non-anastamosing veins, similar to these specimens. Many of the specimens in this study resemble the central portions of the leaves of *E. pseudopteris*. However, some specimens (Plate 3 fig. 2) from the Big Muddy Valley show the more complex leaf shapes associated with *Lygodium*, not coming to distinct separate leaflets with distinct bases. Therefore these specimens are less likely to be *E. pseudopteris*, which exhibits distinct leaflets, and is one of the points that tie these specimens to *Lygodium*.

Lygodium has not been identified in any of the other Saskatchewan or Alberta collections. No explanation has been proposed for this absence, although there is a good chance that this is one of the climatic variation expressions that are expected between the Fort Union Formation floras and more northerly floras.

All extant *Lygodium* spp. are climbing ferns, commonly covering the trunks of trees in the drier areas of *Taxodium* swamps. This interpretation likely applies to the fossil material as well, as remains were found in a locality interpreted as more mesic than many in the area, due to the abundance of roots in the sediments and slightly fewer conifers.

The sterile leaves do not resemble many extant *Lygodium* spp. However, extant species of *Lygodium* show diverse interspecific and intraspecific leaf shape. Only tenative assignment is possible because the fossils found in the current study closely resemble the sterile leaves assigned to *Lygodium* by Brown (1962) and Hickey (1977), which obtained this generic designation through associated sporophylls. However, until sporophylls are found in association, or more ideally connection, to the sterile leaves, no definitive assignment can be made.

Family Thelypteridaceae Pichi-Sermolli

Genus: *Thelypteris* Schmidel

Species: unknown

Plate 4 figs. 1-2

Synonyms and References:

Aspidium goldianum auct. non Lesquereux, 1874.

Lastrea goldianum auct. non (Lesquereux) Lesquereux,1883; Brown, 1962, and all synonymies listed.

Localities: US 817

Figured specimens: US817-9021, US817-9022

Description: Pinna at least 10 cm long. Pinnules are 11.5 mm long 4 mm wide, borne in alternate pairs, sessile on the pinna rachis. Veins arching, unbranched. Margins entire. Two rows of sporangia are present on fertile pinnules, one row on each side of the central vein.

Remarks: A small number of specimens of this plant were recovered from locality US 817. This species was previously unknown from Ravenscrag Formation floras. It is identifiable from its small pinnules with distinctive single dichotomizing veins on the sterile specimens. Fertile specimens have sporangia present near the main vein of the pinnules. The 2 rows of round sori are distinctive for this genus. These specimens resemble *Lastrea goldiana* (Lesquereux) Lesquereux recorded in Brown 1962.

No intact sporangia have been recovered for this species from any collection, which is unfortunate. The initial association with *Lastrea* was based on gross morphology, done in a "picture matching" method, primarily through their comparable appearance to the specimens in Brown 1962. It appears that Brown made his generic assignment through matching his specimens to the modern. According to Collinson (2001), other specimens assigned by Brown to *Lastrea* actually belong to a species of *Thelypteris*, or another genus in the Thelypteraceae, such as *Cyclosorus*. No mention of this species of "*Lastrea*" was made by Collinson. However, a general call was presented in that paper for revisions to many of Brown's (1962) ferns. The present study follows this suggestion and assigns these specimens to *Thelypteris*, which they most closely

resemble, lacking the anastamosing veins of *Cyclosorus* (Collinson 2001). However, future recovery of sporangia may revise generic placement.

The specific epithet of "goldiana" cannot be used for these specimens. *Lastrea goldiana* (Lesquereux) Lesquereux is a junior usage of *L. goldiana* Presl 1836, an extant species that these specimens were being compared to. Additionally, *Thelypteris goldiana* (Hooker) Nieuwland has also been used as a synonym for the same fern in the past. Therefore, a new specific epithet is needed for these specimens. This will require additional study and better specimens, as these poorly preserved specimens are not fully adequate for distinguishing a new species. In 1916, Berry noted that what was called *L. goldiana* had crenulated margins. These specimens do not exhibit these margins, instead having clearly entire margins. This difference may be enough to disassociate them from *L. goldiana*, and are not held in synonymy with the specimens in this study. Optimistically, better specimens will be discovered at another locality to resolve these taxonomic issues, as the formation of a new species is outside the scope of the present project.

Family Incertae Saedis
Unknown fern
Plate 4 fig. 3
Localities: US 817
Figured specimen: US817-9023
Description: Fragment portions of larger leaves are 5 mm wide, and at least 17 mm long. It is unclear how much of the pinnae these fragments represent. Non-sessile pinnules, as the base has been recovered. Simple, non-branching veins arising from the rachis of each of the pinnule fragments, 1mm apart at 60 degrees. Surface striated parallel to veins.

Remarks: Only one rock with two poorly preserved sterile specimens has been recovered from locality US 817. These specimens do not resemble other known ferns from the Paleocene of the Great Plains. However, the venation more closely resembles ferns than other groups of plants. The materials are too fragmentary for identification

beyond placement amongst the ferns. They do not resemble any of the ferns present in other localities, or in the general Paleocene floras of the Northern Hemisphere (Collinson 2001).

Class Gymnospermopsida
Order Coniferales
Family Cupressaceae (Bartlett) Eckenwalder
This includes both the Cupressaceae (ss) and the Taxodiaceae but not the Sciadopytiaceae, as determined through molecular, developmental and morphological studies (Eckenwalder 1976; Brunsfeld et al. 1994; Gadek et al. 2000).

Genus: *Glyptostrobus* Endlicher 1847
Species: *Glyptostrobus dakotensis* Brown 1936
Plate 5, figs. 1-8
Synonyms and References:
Glyptostrobus europaea auct. non (Brongn.) Unger, Newberry, 1898, p. 24-25, pl. XXVI, fig. 8a; Hickey, 1977, p.110-111, pl. 5 figs. 12-14, pl. 6, figs. 1; Hoffman, 2002, p. 31-32, pl. 5, figs. 35-41.
Glyptostrobus dakotensis Brown, 1936, Journ. Wash. Acad. Sci. 26 (9): 355-356 figs. 2, 3; Pabst, 1968, p. 50-51, pl. 12, figs. 1-3.
Cryptomerites lambsii Bell, 1949, p. 49, pl. 29, figs. 2, 4, pl. 30, figs. 1, 3-5, pl. 31, fig. 4, pl. 32, figs. 2, 4.
Glyptostrobus nordenskioldii (Heer) Brown non *Sequoia nordenskioldii* Heer, 1962, p. 49, pl. 11, figs. 3, 7-22 (pro parte, only including the synonymies listed here); Christophel, 1976, p. 17, pl. 6, figs. 35, 37-41, pl. 7, figs. 42, 44, 45, pl. 8, fig. 42, pl. 9, figs. 52-54a, 56, pl. 10, figs. 58-60, pl. 11, fig. 64, pl. 12, fig. 68; McIver and Basinger, 1993, p. 25, pl. 11, figs. 4, 5, pl. 12, figs. 1-6.
Glyptostrobus sp. - Aulenback and LePage, 1998.
Localities: US 817, US 819, US 820, US 821, US 822, US 823, US 825, US 828, US 829, US 830, US 833, US 834, US 835, US 836, US 838, US 839, US 840, US 841, US 842, US 843

Figured specimens: US817-9024, US820-9025, US821-9026, US838-9027, US840-9028, US817-9029, US817-9030, US828-9031

Description: Foliage cupressoid to taxodioid, alternately arranged; sheathing bases, quadrangular in cross section; foliage on shoots subtending the cones crypto-cupressoid; Ovulate cones terminal on shoots bearing cupressoid to cryptocupressoid leaves on otherwise undifferentiated shoots, at least 5 mm long; cones globose to pyriform, 8-17 mm long, 6.5-15 mm wide. 12-21 ovuliferous scales per cone, helically arranged, arising from a basal disk. Scales triangular to flabelliform, 5-15 mm long, 3-11 mm wide, with a rounded, acute or cordate margin, with (0-) 5-11 (-17) uneven marginal teeth; bract forms a prominent mucro on the abaxial face of the scale immediately proximal to the flaring point of the scale, 3-7.5 mm in width, initiating larger than the scale in forward orientation, becoming reflexed with age; cones contain fertile and infertile scales, fertile scales bear 2 seeds; seeds with one large wing attached obtusely to the basal nutlet, born upright on the adaxial surface, leading to 2 prominent scars.

Remarks: Appendix A covers a revision of Paleogene *Glyptostrobus*, which incorporates the fossils from this study into its data set. It clarifies the taxonomy of these specimens. Based on the work conducted in that study, these materials have been placed into *G. dakotensis*.

Cones with foliage are found in nearly every locality in the area. It is expected that additional collections would reveal cones in all of the localities where cones have not been recovered. All of the localities without cones have only limited collections, likely underrepresenting the full floral composition. Found in the majority of localities, those yielding *Glyptostrobus* typically have it as the commonest element. In others, it is the second or third commonest element. It is notably absent from locality US 832, which typifies the third sub-flora.

Genus: *Metasequoia* Miki

Species: *Metasequoia occidentalis* (Newberry) Chaney

Plate 6, figs. 1-3

Synonyms and References:

Taxodium occidentalis Newberry, 1863, p. 516; 1868, p. 45.
Metasequoia occidentalis Chaney, 1951, and all synonymies listed; Chandrasekharam, 1973; Christophel, 1976, and all synonymies listed; Hickey, 1977; McIver and Basinger, 1993; Liu et al., 1999, and all synonymies listed.
Localities: US 817, US 822, US 828, US 830, US 840, US 843
Figured specimens: US843-9032, US828-9033, US843-9034
Description: Leaves decussate, taxodioid with small petioles, bases rounded to acute. Prominent central vasculature, apex rounded or acute. 1-3 mm in width, 3-25 mm in length, with length to width ratios mostly 4:1 to 10:1, although a few specimens near 20:1. Seed cones borne terminally on a peduncle, at least 10 mm in length till the first node, 2.5 mm wide. Seed cone globose, 14-17 mm wide, 16-18 mm long (1:1 length to width ratio). Bract-scale complexes are likely decussate in 4 rows, although the number of rows is difficult to determine as the seed cones are poorly preserved casts; each bract-scale is peltate, with faces 10 mm wide, 3mm tall.

Remarks: Foliage assigned to *Metasequoia occidentalis* is an uncommon member of most of the localities throughout the collection area, found in the basal beds of the Ravenscrag Formation. It is dominant in a few beds of a few of these localities (e.g. US 843, US 828), with greater abundance of specimens present in the localities on the north face of the valley, and those near Big Muddy Lake. It is commonly found in association with *Glyptostrobus*/*Elatocladus*. Cones are rare. The identification of this taxon from localities US 817, US 822 and US 840 is by purely foliar evidence. *Metasequoia occidentalis* is a member of these localities. A number of shoots have been recovered from US 822, but less than 10 have been seen from US 817, and only one fragment is recorded from US 840. This light distribution was anticipated by the precedent at the Ravenscrag Butte type section (McIver and Basinger 1993), whereas the heavier distribution correlates well with other collections where *Metasequoia* is the dominant conifer (for example Basinger 1991).

When establishing this species, Chaney (1951) discussed the difficulties of assigning fossil foliar specimens to *Metasequoia* and other members of the Cupressaceae (s.l.). Chaney concentrated on *Sequoia* sp. and *Taxodium* sp. in his discussion, and

devised a method of differentiating these taxa via leaves. Christophel (1976) continued this work and added *Glyptostrobus* sp. to this analysis. They concluded that it is difficult to distinguish *Metasequoia* from other closely related taxa without a large sample size, as the characteristics overlap. However, as a number of foliar specimens, and, more importantly, seed cone specimens with leafless supporting shoots, are present in the beds of the present study, a designation of *Metasequoia* can be confidently made in these localities. Within this large sample base, *Metasequoia* foliage is distinct from all other taxodiaceous foliage due to its decussate phyllotaxy, and can therefore be confidently assigned to this genus. In the future, if foliage of this form is found attached to seed cones of another morphology, then this designation will need to be reconsidered. Based on the present evidence the remains closely resembles extant *M. glyptostroboides* Hu and Cheng, and may in fact be the same biological species. However, it is impossible to say that for sure due to the asynchronous occurrence of these two taxa. It is also not clear whether these belong to the same species as other fossil *Metasequoia*.

These specimens conform to our understanding of the taxon provided by the synonomies, but do not add any amendments to the taxon. The scales of the seed cones do appear to be opposite one another and not alternate, which is an arrangement noted recently in *Metasequoia foxii* Stockey et al. 2002. In that paper, they felt that only one species of *Metasequoia* was present, and because the cone scale arrangement was for the most part distinct considered the specimens to belong to another species. However, specimens from a number of closely related localities in the Buchanan Lake Formation on Axel Heiberg Island, Nunavut challenge that conclusion. An ongoing, detailed assessment of this collection has produced numerous cones with both cone scale arrangements collected from within the same forest floor litter. The typical decussate arrangement dominates, but alternate cone scaled cones make up a notable minority (Y. Liu and J.F. Basinger, personal communication 2002). There are two possible conclusions that can be drawn from this information. The first, that *Metasequoia* grows in mixed species stands where the characters of the two taxa overlap extensively other than in cone scale arrangement. The second possibility is that the diagnosis of *M. occidentalis* should be expanded to include production of alternately arranged cones. A concurrent study of *M. glyptostroboides* foliage has indicated that alternate cone scale

arrangement in the cones may be present in the extant species (Y. Liu and J.F. Basinger, personal communication 2002). If this is the case, then the second option is likely, at which point it seems likely that *M. foxii* will be considered a junior synonym of *M. occidentalis*. Conversely, if the first option is correct, then there is a distinct possibility that some of the non-coning (especially seed cone) material of the present study may belong to *M. occidentalis*. This may again amend the taxa. Whatever the outcome, it seems most prudent to place these fossils in *M. occidentalis*, as they are primarily foliar specimens that occur within the agreed range of this species. The one exception to this may be one specimen that has bluntly pointed apecies. Considering that all other known species of *Metasequoia* include individuals with bluntly pointed apecies, it seems better to amend *M. occidentalis* to also include specimens with this morphology. Unpublished specimens from the Eocene of Ellesmere Island confirm this, along with a larger leaf size. These specimens are assigned to *M. occidentalis*, as they were collected with decussate cones.

Genus: *Elatocladus*
Species: *Elatocladus megasequoiae* sp. nov.
Plate 6, figs. 4-5
Diagnosis: Leaves linear to oblong to lanceolate, opposite distichous (perhaps alternate) phyllotaxy. Accute tips (bluntly pointed), single well developed vascular trace, petiolate obtuse bases. Leaves 5-10 mm wide, 60-80 mm long.
Holotype: Plate 6, fig. 4
Etymology: Leaves resemble *Sequioa* sp. and *Metasequoia* sp., but are notably larger.
Localities: US 828
Figured specimens: US828-9035, US828-9036

Remarks: Only foliage was recovered in the present study and was restricted to locality US 828, where it was found in beds with *Glyptostrobus*, *Metasequoia*, *Ettingshausenia* and *Cercidiphyllum*. The morphology is similar to *Metasequoia occidentalis*, but is much larger than any known *M. occidentalis* specimens. Like *Metasequoia*, *Elatocladus megasequoiae* exhibits distichous phyllotaxy, although, also like *Metasequoia*, it may in

fact be pseudo-distichous. However, some of the recovered specimens appear to have alternate phylotaxy, although it is equivocal due to the fragmentary nature of the fossils. *Metasequoia occidentalis* is well known from Paleocene beds of North American basins, with a consistent size range of 10 mm to 25 mm, although unpublished specimens have been found in Eocene deposits on Ellesmere Island with leaves 38 mm long. Also, specimens labelled *M. foxii* Stockey et al. (2001) have leaves up to 43 mm long. *Metasequoia glyptostroboides* is known to have foliage up to 45 mm in length. It is possible that the leaves of the present study are large specimens of *Metasequoia* spp. Unfortunately, no coning material or cuticles were recovered to allow for comparisons with the genera of the Cupressaceae to confirm this hypothesis.

These specimens could possibly be placed in *Elatocladus olriki* (Heer) Bell, a taxon which derives from *Taxodium olriki* Heer. *Elatocladus olriki* is a composite taxon that has included specimens of *Taxus*, *Taxodium* and *Metasequoia* as well as extinct genera (Brown 1962). With the recognition of *Metasequoia* (Chaney 1951), this taxon has largely fallen out of use. The fact that much of this taxon was placed in *Metasequoia occidentalis* when it was first erected supports the idea that these leaves could be placed here, in recognition of the resemblance to *Metasequoia* fossils.

It is premature to assign these leaves to any other known genus without definitive seed cones. Future projects may recover such definitive attached cones, or more complex shoot structures, showing smaller known conifer leaves attached to these larger ones to demonstrate the needed identification.

It has been suggested that these specimens may belong to a species in the Podocarpaceae (E. Leopold, personal communication 2006), as the leaves fall within the range of sizes for this family, whereas they are beyond the size expected for any member of the Cupressaceae. However, strong supporting evidence such as reproductive materials, cuticles or an extensive pollen record in the region would be necessary to consider this link. The few reports of North American Podocarpaceae (Dilcher 1969; Reinink-Smith and Leopold 2005) have been challenged. No pollen sample from US 828 has been collected, but palynological samples from the region have not included Podocarpaceae. More specimens would be necessary to consider this possibility.

Genus: *Mesocyparis* McIver and Basinger

Species: *Mesocyparis borealis* McIver and Basinger

Plate 7 fig. 1-4

Synonyms and References:

Mesocyparis borealis McIver and Basinger, 1987, p. 2340, figs. 4-7, 10-21, 35-43; 1993, p. 30, pl. 14, figs. 1-5.

Localities: US 817, US 822, US 826, US 832, US 840

Figured specimens: US840-9037, US826-9038, US832-9039, US840-9040

Description: Branching opposite, forming flat sprays. Stem width 2.5 mm in proximal areas. Lateral branching 3 mm apart, at every lateral internode in branching portion. Up to 10 branching events creating branchelts. Branchlets unbranched. Seed cones borne laterally in the same plane as the lateral leaves, as well as other branching events, proximal to the branchlet areas, distal to the scale leaf areas. Up to 6 cone pairs per branch, 5-10 mm between each coning node. Leaves are opposite in 4 ranks, persistent. Branch leaves distinct from branchlet leaves. Facial leaves distinct from lateral leaves. Branchlet facial leaves ovate, cupressoid, 1.2-2.1 mm wide, 1.5-3.5 mm long, acute tips, midrib somewhat prominent. Branchlet lateral leaves folded along midrib, cupressoid, 1 mm wide, 2-3 mm long, acute tips. Up to 10 whorls of leaves per branchlet. Distal branch facial leaves largely imbricate, 10 mm long with 1 mm free at the tip, acute apex. Distal branch lateral leaves folded along midrib, 2.3-3 mm free, at least 2 mm additional imbricate, cryptocupressoid. Proximal branch leaves cupressoid, 1.2 mm wide, 1-3 mm long, acute tipped. There is little difference between facing and lateral leaves. Branches also with proximal type leaves. Seed cones terminal on shoots 1mm in length. Seed cones globose, 3-5 mm wide, 3-6 mm long, 4 bract-scale complexes per seed cone. Seed cone scales 2-3 mm wide, 2-3 mm long. Bracts emerge as umbos, 1.5 mm wide, 1 mm long. Scale margin lightly incised, with 13 teeth.

Remarks: *Mesocyparis borealis* is only known definitively from the Paleocene deposits of the Great Plains of the Western Interior of North America. Foliage of the type assigned to this taxon has been collected in many localities and placed in the morphogenus *Cupressinocladus*. Fertile remains were first discovered at Ravenscrag

Butte in the Cypress Lake map area (McIver and Basinger 1987). The fertile remains are unlike any extant species of the Cupressaceae, especially in orientation of the seed cones. It most closely resembles *Chamaecyparis* (McIver and Basinger 1987), but is distinct from that genus. This taxon illustrates the difficulties associated with using modern analogs for generic names amongst fossil groups. Foliage of this form was often placed in *Thuja* in the early explorations of these beds (McIver and Basinger 1987). There are also similarities, primarily in organ arrangement, with the Southern Hemisphere Libocedrae.

The material collected from the Willow Bunch Lake map area closely resembles the type material from Ravenscrag Butte. No seeds or pollen cones were recovered from the Willow Bunch Lake map area. Specimens of *Cupressinocladus interruptus*, a morphospecies used for specimens bearing *Mesocyparis*-like foliage, without the diagnostic reproductive organs, are rare members of some of the localities near Highway 34 (US 817; US 822). These will be placed in *Mesocyparis borealis* as well as the specimens with seed cones found at other localities, as the foliage appears identical to the *M. borealis* with seed cones found at the other localities in this study. In the two areas above the Hart Coal Seam (US 832 and US 840), *Mesocyparis* is the dominant conifer. In locality US 832, it is the only conifer, although it is rare in the overall flora of this site. In locality US 840, it is the dominant member of a select layer. When *Mesocyparis* has been recovered in this area, it is common to find it in monotypic, or near so, beds. This is likely indicative of an alternate environmental setting than that of *Glyptostrobus*/*Trochodendroides* flora, which is common in much of the area.

Three species have been described: *Mesocyparis borealis* McIver & Basinger and *M. umbonata* McIver and Aulenback from the western North American sediments of Paleocene and Cretaceous age respectively; and *M. beringianum* (Goloneva) McIver and Aulenback, and *M. rosanovii* Kodrul, Tekleva and Krassilov from the late Cretaceous of northern Russia. . Of these species, the present specimens most closely resemble *M. borealis*. The branching is opposite in a single plane in all specimens of the present study except one, which is ambiguous. This is distinct from *M. umbonata*, where a significant percentage of specimens have decussate branching, especially the

arrangement of the origination of seed cone axes. Additionally, the specimens from the present study are also closest in both time and space to the Ravenscrag Butte material.

These specimens vary from the type material of ***M. borealis*** in a number of subtle ways. The seed cones are consistently on the small end of the size range for the type locality, and are spaced further apart on the cone axis. These differences likely reflect variability between populations rather than taxonomic discinctions.

Common practice is to use *Cupressinocladus interruptus* as a morphospecies for infertile remains. This practice is appropriate, as foliage of this form resembles many extant genera and species of the Cupressaceae. Also, it is difficult to differentiate between *Mesocyparis* species in the absence of cones. It is quite likely that there were multiple genera with foliage of this type in the Early Paleocene of North America. Infertile remains would best be placed in *Mesocyparis* only if fertile remains are discovered in the vicinity, and the beds are monotypic. If there is any ambiguity, ***C. interruptus*** should be used instead. The practice of utilizing ***C. interruptus*** limits our deliniation of *Mesocyparis* distribution, but seems the only safe way to account for those specimens. However, the large number of *Mesocyparis borealis* specimens found in this study at all stratigraphic levels eliminates the need to use *Cupressinocladus interruptus* for specimens from this study.

Genus: *Corvirupestrobus* gen. nov.
Diagnosis: Isolated seed cones, thought to be terminal on shoots. Conescales arising from a central axis. Bract scale complexes wedge shaped non-peltate with emergent mucronate bracts, slightly flabelliform with small marginal teeth. Complete cones resembling *Cryptomeria* sp. and *Glyptostrobus* sp.
Etymology: "Raven's Crag Cones", named for the Ravenscrag Formation.
Generitype: *Corvirupestrobus adrielensis* sp. nov.

Species: *Corvirupestrobus adrielensis* sp. nov.
Plate 8, figs. 1-6
Diagnosis: Isolated seed cones. Outline is globose to cylindrical. Cone size is 16-19 mm length, 14-18 mm width. at least 8 cone scales arising from a central axis, arise in 4

whorls. Wedge-shaped, non-peltate bract scale complexes that have the bracts as prominent mucros, up to 9 mm in length and up to 8 mm in width, with striated inner surfaces, marginal teeth.

Holotype: Plate 8, fig. 1 (USPC 9041)

Etymology: Named for Mr. Adriel Larson of Bengough, SK, who found the type specimen and helped orchestrate this study.

Localities: US 840, US 822 (US 821?)

Figured specimens: US840-9041, US840-9042, US840-9043, US840-9044, US840-9045, US822-9046

Remarks: Found primarily in the sub-flora 2, where it is an uncommon element. However, a few poorly preserved specimens found in US 822 and US 821 show that it was also a rare element of sub-flora 1. Identification can be difficult. No foliage has been definitively assigned, although some cryptomeroid leaves may belong to the plant. Individual cone scales resemble extant *Cryptomeria* and *Glyptostrobus*. However, the complete central axis shows closer affinity to *Cryptomeria* than *Glyptostrobus*, although the form of the scales more closely resembles *Glyptostrobus*. A cone with a visible central axis is necessary to clearly deliniate specimens as not *Glyptostrobus*. *Cryptomerites* has been used as a morphogenus for plants like this in the past, but due to later synonymies and complications, this genus is no longer valid. Therefore, *Corvirupestrobus*, a new genus, is being erected for these purposes.

This material bears some resemblance to material described as *Fokienia ravenscragensis* McIver and Basinger, in particular the specimens from Alberta published by McIver and Aulenbeck (1992). This species, as initially designated, resembles extant *Fokienia*, which bears oppositely arranged peltate scales. However, the Alberta specimens are described with semi-peltate scales, which resemble to a degree the non-peltate scales present in the specimens analyzed here. Associated foliage becomes an important factor, as these cones much more closely resemble extant *Cryptomeria* than extant *Fokienia*. In other localities, *Fokienia ravenscragensis* cones are associated with *Fokienia* foliage, often classified when isolated as *Fokieniopsis catenulata* (Bell) McIver and Basinger. No *Fokienia*-like foliage has been found in the

present study area. However, some of the branches tentatively assigned to *Glyptostrobus* that are present in the localities where these cones are prevalent resemble *Cryptomeria*, as they have cryptomeroid leaves exclusively, and appear with a slightly different texture than the associated *Glyptostrobus* foliage. This raises the possibility that these are cones of a *Cryptomeria*-like plant. Future exploration is needed to develop a resolution to the affinities of these cones, as attached foliar shoots should provide a definitive answer.

The presence of these cones complicates identification *Glyptostrobus dakotensis* material, as it makes the normally diagnostic cones and seed cone scales more difficult to use for positive identification. However, once identified, subtle differences become diagnostic. These cones have less overlap in their scales, as the scales do not share a common point of origin. The mucronate bracts are longer and more pronounced than Paleogene *Glyptostrobus* specimens. The inside of the scales have striations, which are lacking in *Glyptostrobus* scales. Additionally, the scales are slightly woodier than *Glyptostrobus*, which facilitates sorting when specimens of both are found in a locality.

Class Angiospermopsida
Order Typhales
Family Sparganiaceae F. Rudolphi
Genus: *Sparganium* L.
Species: unknown
Plate 9, figs. 1-2
Localities: US 832 (US 822?, US 820?, US 834?)
Figured specimens: US832-9047, US832-9048
Description: Globose inflorescences, 8 mm in diameter. Borne terminally on 10 mm long shoots. Shoots are part of larger panicles of at least 3 inflorescences, with at least 10 mm between nodes.

Remarks: These inflorescences are found definitively only in US 832, although there is some question whether they appear elsewhere, as they resemble both *Sparganium* sp. and *Ettingshausenia* sp. At US 832 there are no platanoid leaves present, rather there

are elongate, strap-shaped monocot leaves that at least superficially resemble *Sparganium* (described as a separate taxonomic entry below). Therefore, it is likely that these represent the inflorescences of *Sparganium* or something *Sparganium*-like. The individual heads most closely resemble *Sparganium parvum* Hickey. However, they differ from *S. parvum* in having long peduncles.

Isolated globose structures were found in other localities but without the long leaves that are assumed to be the foliar elements of these plants. These inflorescences may or may not be the same species, as this association is somewhat important to familial designation, as globose catkins of this type are common in many angiosperm families. Notably, the staminate inflorescences of the Platanaceae appear similar. However, the lack of clustering in the reproductive organs suggests affinity to *Sparganium*, as other genera with similar globose inflorescences feature clustering to their reproductive organs.

Unknown monocot leaves
Plate 9, fig. 3
Localities: US 822, US 832
Figured specimen: US832-9049
Description: Elongate leaves with parallel venation. Leaves 3 cm wide; undetermined length. Specimens over 20 cm long are common, with no apparent taper to estimate length. Leaves often found overlapping one another.

Remarks: These specimens are from a monocot with long leaves, likely resembling a rush. The presence of inflorescences resembling *Sparganium* supports this interpretation. They are common elements in US 832. They are likely *in situ* elements of this locality, whereas the other elements are interpreted as being transported to the site. Fragments of elongate parallel veined leaves also occur in the *Nelumbago* beds of locality US 822. It is unclear whether these are the same species as the US 832 specimens due to the highly fragmentary nature of the US 822 specimens.

These leaves often resemble woody branches, which are a rarer element of the third sub-flora than the numbers that appear in the first sub-flora. The dichotomies present on these leaves are a distinct feature, as are the obvious venations.

Strap-shaped monocot leaves are common elements of many reports from similarly-aged floras (Hoffman 2002; McIver and Basinger 1993). The definitive affinities of these plants beyond an association with the Monocotyledons are not usually attempted, as many families bear leaves of this form without readily observable distinguishing features. Ambiguity leads containment as unknowns. Despite the associated inflorescences identified as *Sparganium* sp. (described above), it is safest to follow this practice for the leaves of the present study as well, at least until attached fertile specimens are found. In the present fossils, an association between these leaves and the inflorescences identified as *Sparganium* sp. is not definitive, as many other plants produce inflorescences that closely resemble those inflorescences in question.

Order Incertae Saedis

Genus: *Paloreodoxites* Knowlton

Species: *Paloreodoxites plicatus* (Lesquereux) Knowlton

Plate 9, fig. 4

Synonyms and References:

Oreodoxites plicatus Lesquereux, 1883, p. 122, pl. 18, figs. 1-4; Knowlton, 1917, p. 287, pl. 63, fig. 1.

Paloreodoxites plicatus (Lesquereux) Knowlton, 1930, p. 41, pl. 11, figs. 1-4; Brown, 1956, p. 208, pl. 33, fig. 5; Brown, 1962, p. 54, pl. 15, figs. 3, 7; Read and Hickey, 1972, p. 135; Peppe et al., 2007, p. 562, figs. 13-4.

Localities: US 844

Figured specimen: US844-9050

Description: Heavily striated leaves or bundles of leaves, with parallel ridges and parallel veins. Each structure is over 20 mm wide, over 120 mm long. The remains are fragments of larger structures.

Remarks: These large striated structures occur in one ironstone layer in the study area, locality US 844. This bed is interpreted as earliest Paleocene, but may be latest Maastrichtian, as the marker coal layers are not obvious in the section where the specimens were collected. However, according to GPS elevation readings of both the marker beds and these beds, these beds occur about 10 m above the marker bed, placing them in the Paleocene, and therefore the Ravenscrag Formation. This species does not help to resolve the stratigraphic issue, as it crosses the K-T boundary.

These structures are widely considered monocots (Brown 1962; Knowlton 1930; Read and Hickey 1972; Peppe et al. 2007) somewhat related to palms (Arecaceae), although their exact affinity is debatable. It is thought that they are a close outgroup to the palms. These leaves lack the structural organization needed to be considered true palms (see Read and Hickey 1972).

This species is rarely found, and this is the first report of this species from the Ravenscrag Formation. Specimens in this latitudinal zone are previously unknown. They occur more frequently farther south (Brown 1962) or nearer the epicontinental seaway (Peppe et al. 2007). This is the farthest north occurrence of this species. Its presence is somewhat anomalous, given the rest of the flora, which trends towards the floras further north than those to the south, with deciduous conifers and broad leaved floras common.

Subclass Magnoliidae

Order Nelumbonales

Family Nelumbonaceae Dumotier

Genus: *Nelumbago* McIver and Basinger

Species: *Nelumbago montanum* (Brown) McIver and Basinger

Plate 10, figs. 4-5

Synonyms and References:

Nelumbium montanum Brown, 1962, p. 69, pl. 35, figs. 2-4; Johnson, 2002, (FU62) p. 367, pl. 15, fig. 4.

Nelumbago montanum McIver and Basinger, 1993, p. 33-34, pl. 19, figs. 4, 6, and all synonymies listed.

Localities: US 822, US 929

Figured specimens: US822-9054, US822-9055

Description: Specimens circular to reniform unattached simple leaves; mesophylls to macrophylls up to 16.5 cm diameter. Leaves peltate to eccentric-peltate, petiolar attachment. Peltate leaves lack bases and apices. Margin entire, unlobed. Venation radiating, either in an arc from a marginal edge or from a central point. Veins dichotomizing multiple times throughout length. Radiating veins brochidodromous. Tertiary veins random reticulate.

Remarks: These remains were only recovered from one bed (US 822(1)), in the 2003 and 2004 field work, which contains this species almost exclusively. Specimens are also stored in the USPC collections from 1992. Numerous sizes of leaves are found at locality US 822. The matrix of the rock preserving these leaves is fissile, so it is difficult to remove specimens of any size. Therefore, figured specimens from the Nelumbago bed of locality 822 are partially stored in the Bengough collections, unlike the other taxa of this study. This plant is identifiable by its numerous dichotomizing radiating veins, either from a marginal or central origin. Numerous other species of this genus and related genera are described from across the Great Plains and are mentioned in Berry 1935. The genus *Nelumbago* was erected for this species, as all earlier proposed genera were not able to be used. These specimens did not match the generitype diagnosis for *Nelumbites* Berry and not being available as a specific name in the case of *Nelumbium* A.L. Jussieu due to it being an orthographic variant of *Nelumbo.*

This species was a floating aquatic. That the specimens were recovered from a nearly monotypic bed inidicates that the plants thrived in a unique habitat compared to other plants, likely in a deeper water environment, where *Glyptostrobus* was unable to become established. *Nelumbago* is typically found in these monotypic beds, so limited distribution is expected (McIver and Basinger 1993).

No reproductive materials were recovered for this plant in this study, and only a few proposed structures have been recovered at all (Brown 1962). There is some controversy to the assignment of these materials, with a distinct possibility that they are not the reproductive materials for this plant. Regardless, they do little to elucidate

taxonomic affinity of these plants. In these localities, there is an expected variance amongst the leaves, primarily in placement of petiole attachment. Some specimens exhibit central attachment, whereas others exhibit lateral attachment.

Order: Incertae Saedis
Genus: *Paranymphaea* Berry
Species: *Paranymphaea crassifolia* (Newberry) Berry
Plate 10, figs. 1-3
Synonyms and References:
Catalpa crassifolia Newberry, 1868, p. 56.
Paranymphaea crassifolia (Newberry) Berry, 1935, p. 39, pl. 7, figs. 4, 5, pl. 9, pl. 10; McIver and Basinger 1993, p. 39, pl. 25, pl. 26, figs. 1-3, and all synonymies listed; Johnson, 2002, (FU1) p. 364, pl. 15, fig. 1; Barclay et al., 2003, p. 71, fig. 9D, 9E.
Localities: US 820, US 822, US 838, US 845, US 928, US 933
Figured specimens: US845-9051, US822-9052, US822-9053
Description: Specimens unattached simple leaves, deltoid in shape. Leaves have cordate bases and acute apices, and have bilateral symmetry. Leaves not lobed and margins entire. Length to width ratio 1:1 to 2:1. Stout petioles common, at least 28 mm long; arise nearly perpendicular to the blade. Primary venation basally actinodromous, with at least 5 basal veins. Secondary veins festooned brochidodromous, with compound agrophics, irregular spacing and strong inter-secondary veins. Tertiary veins opposite convex percurrent, obtuse to primary (nearly parallel), and maintain this obtuse angle uniformly. Quaternary veins regular polygonal reticulate. Fifth order veins regular polygonal reticulate with well developed 4-sided areolation. Free ending veins are absent. Fifth order veins are the highest visible vein order, as well as the highest excurrent order. Exhibits fimbrial veins. Leaves exhibit 4r organization. Texture chartaceous without cuticle.

Remarks: *Paranymphaea crassifolia* is a rare element of this flora, but it appears in many localities in the area. Only in section US 845 is it abundant, where a wide variety of morphologies are present. All specimens recovered from the area show the distinct

venation, and all specimens where the base is preserved show the clear cordate base typical of this species.

Paranymphaea is common in the Ravenscrag Butte collections and in similarly-aged floras found to the south. Its general rarity in the Big Muddy Valley is notable, especially as it is commonly associated with the general *Glyptostrobus* swamp floras that dominate the area in other localities. The ecological niche of *Paranymphaea* is questionable. McIver and Basinger (1993) propose the lifestyle of a forb, a non-aquatic lower story plant, partially based on a perceived tie to the Polygonaceae. However, this interpretation was also supported by the thin vernation and absence of aerenchyma of the leaves, and the possibility that the leaves had stomata on both surfaces. However, the distribution in this study somewhat contradicts this interpretation as they are primarily found in beds containing only aquatics. Although the reasoning presented by McIver and Basinger is sound, this distribution cannot but raise doubts to its validity, and instead supports earlier interpretations of *Paranymphaea* as an aquatic or semi-aquatic plant.

Paranymphaea has a limited stratigraphic span in the latest Cretaceous and Early Paleocene. This age is in conformity with the standard interpretation for the localities in this study where these remains were found. No *Paranymphaea* remains were found in the Mid Paleocene or Late Paleocene localities examined in this study.

The venation of *Paranymphaea* is difficult to describe using the Leaf Architecture Working group descriptors, as there is an obvious primary with secondaries (that approaches a pinnate arrangement), but there are palmately radiating veins of a comparable size to the primary originating at the insertion. These secondaries appear to give this leaf a palmate venation, but act like secondaries, looping in a fashion similar to later originating secondaries.

Some leaves found in conjunction with *Nelumbago montanum* in locality US 817 may be *Paranymphaea*, although they lack the presence of both the base and apex in a single specimen, assuming that either is present (pl. 10 fig. 2). The venation resembles *Nymphaea* and *Paranymphaea*, consisting of festooned brochidodromous venation. These leaves may be peltate, based on orientation, although this is speculative. Stems (pl. 10 fig. 3) appear on the same sample as one of the specimens. They are thick

enough to be *Paranymphaea* petioles, but may instead be *Nelumbago montanum* stems or another aquatic.

Subclass Hamamelididae
Order Hamamelidales
Family Platanaceae T. Lestiboudois ex Dumortier
Genus: *Ettingshausenia* Stiebler.
Species: *Ettingshausenia raynoldsii* (Newberry) Moiseeva
Plate 11, figs. 1-2; pl. 12, figs. 1-2
Synonyms and References:
Platanus raynoldsii Newberry, 1868, p. 69; Brown 1962, p. 64, pl. 30, figs. 1-4, pl. 31, figs. 1-6, pl. 66, fig. 8, and all synonymies listed; Chandrasekharam 1974; Christophel 1976.
Ettingshausenia raynoldsii (Newberry) Moiseeva, 2008, and all synonymies listed.
Localities: US 828, US 826, US 822, US 834, US 831, US 841 (US 820?, US 817?)
Figured specimens: US828-9056, US828-9057, US826-9061, US826-9062
Description: Mesophyll to macrophyll leaves; some specimens over 20 cm wide and 20 cm long. Remains of large leaves fragmentary; therefore, maximum leaf size unknown. Symmetrical, elliptic lamina; approximate length to width ratio of 1.1:1. Bases are largely concavo-convex, apices convex; leaves have an obtuse base angle and obtuse apex angle. Leaves palmately trilobed, with serrate margins. Primary veins palinactinodromous. Secondary veins craspedodromous. Numerous compound agrophics. Three basal veins. Secondary vein spacing is uniform, as is secondary vein angle. Inter-secondary veins are absent. Tertiary veins convex, opposite percurrent, which are perpendicular to obtuse to the primary vein, increasing exmedially. Quaternary veins regular polygonal reticulate with well-developed areolation. Marginal veins have incomplete loops. Leaf organization is 3r. One order of teeth, frequency of 1 tooth per 1.5 cm. Tooth shape concave-concave with rounded sinuses and simple tooth apices.

Remarks: *Ettingshausenia raynoldsii* (Newberry) Moiseeva is a common element of the *Glyptostrobus* swamp sub-flora. Numerous forms of the polymorphic leaves of this plant have been recovered, reflecting only part of the diversity expected for this species.

Many of the specimens resemble *Platanites canadensis* McIver and Basinger (1993), from Ravenscrag Butte. The new specimens differ in the absence of compound leaves, as there is no evidence of the basal leaflets in the material of the present study. This similarity between the two taxa is mentioned in the initial designation of *P. canadensis*. In 2004, workers on the platanoids of the Far East reconsidered specimens from the Amur region, and found that there were epidermal and macromorophological differences between extant *Platanus* L. and many of the Cretaceous and Paleocene plants that had been placed in that genus, which resulted partially in the transfer of *Platanus raynoldsii* Newberry to the genus *Ettingshausenia*.

The platanoids exhibited a wide variety of morphologies during the Paleocene. *Macginitea* Wolfe and Wehr contains platanoids with obvious lobing, the most extreme specimens exhibiting palmately compound leaves. *Macginitea* is much more common to the south of the Big Muddy localities. Variation in platanoid leaf form is one of the latitudinal changes in the floras of the coal swamps of the Paleocene. Variation in morphology is associated with other names. Besides the apically lobed leaves, compound leaves and leaves with complex basal margins are common.

Platanus, and the other closely related late Cretaceous/Paleogene genera, such as *Macginitea*, *Erlingdorfia* (Brown) Johnson and *Platanites* Forbes, are suspected of being early recovery or pioneer trees in disturbed landscapes, along with the cercidiphyllids (Hoffman 2002); therefore, a large presence of platanoids is considered indicative of a disturbed environment. Since they grow in these challenging terrains, they are often found near the relatively inhospitable swamps, although it is thought that they do not live in the water like the other common elements.

There is a possibility that the remains lumped under this one foliar species belong to more than one species. There is a great variance in size between the small leaves and large leaves that are reported here. However, a large range in size is reported for other fossil species and extant species of *Platanus* L. Therefore, this range likely

represents a variety of morphologies reflecting growth location within a single species versus variations between species (Brown 1962).

Genus: *Macginicarpa* Manchester 1986
Species: unknown
Plate 11, fig. 3-5
Localities: US 834 (US 820?, US 830?)
Figured specimens: US834-9058, US834-9059, US834-9060
Description: Isolated spherical inflorescences, 10-20 mm in diameter, born on 5 mm peduncles. Inflorescences consist of numerous carpals arising in small clusters (likely of 5). Carpels with long hooked styles. No evidence for basal carpellary hairs.

Remarks: Several specimens were found in locality US 834, with one clear specimen from US 830. These appear to be the isolated inflorescences of one species in the Platanaceae. As these are compression specimens, anatomy is indeterminable. However, the long structures more closely resemble styles than anthers and the styles are clustered.

These specimens resemble other *Platanus* inflorescences from localities across the Great Plains, such as *Macginicarpa manchesteri* Hoffman from Joffre Bridge and *Platanus* sp. from Ravenscrag Butte (McIver and Basinger 1993). Differences between *Macginicarpa* and *Platanus* include the absence of dispersal hairs on the achenes in *Macginicarpa*, as well as stylar clustering due to a more developed perianth in the inflorescence (Manchester 1986). The clustering is usually in groups of 5 carpels (Manchester 1986). This difference is more notable in permineralized specimens, as found in many of the generitype specimens of *M. glabra* Manchester. However, the clustering can still be noted in impressions, as *Platanus* will have an even dispersal of styles around the inflorescence, whereas *Macginicarpa* will have clusters around the margin (Manchester 1986). The specimens found in this study often exhibit the styles in clusters, and none of the limited collection shows evidence for dispersal hairs.

Macginicarpa was initially described as associated with *Macginitea* Wolfe and Wehr. The associated leaves in this study are of a *Platanus* type, with no true lobing

evident in any specimens. However, the intermediate *Platanus* species, ***P. nobilis*** Newberry, which has partial lobes, has been associated with *Macginicarpa* in Joffre Bridge materials (Pigg and Stockey 1991). Therefore, the lack of *Macginitea* leaves in the Big Muddy Valley should not be a detriment to using *Macginicarpa*. However, it may be that there should be more genera for platanoid inflorescences.

The six or so inflorescences found in this study are too poorly preserved and incomplete to establish species. Distribution of the inflorescences on the shoots is considered important for classification. However, the inflorescences were all found individually in this study. It is assumed that these are the inflorescences of the abundant platancaceous remains of this study area.

Order Fagales

Family Fagaceae Dumortier

Genus: *Fagopsiphyllum* Manchester

Species: *Fagopsiphyllum praegroenlandicum* (Berry) comb. nov.

Plate 13, figs. 1-4

Synonymies:

Quercus praegroenlandica Berry, 1935, p. 26-27, pl. III, figs. 3-7.

Localities: US 840, US 822, US 817

Figured specimens: US840-9063, US840-9064, US822-9065, US840-9066

Original Diagnosis (Berry 1935, pp. 26-27): "Leaves of medium size, ovate-lanceolate in general outline, with pointed tip and broadly cuneate base. Except at the base the margin shows coarse dentate teeth, which decrease in size distad. Length up to 12 centimetres. Maximum width up to 5 centimetres. Texture sub-coriaceous, Petiole stout, curved, about 1.5 centimetres in length. Midvein stout and prominent. Secondaries about 15 subparallel pairs (occasionally one of the lower ones will fork at or near the base), diverging from the midvein at wide angles, regularly spaced, rather straight, craspedodrome. Tertiary venation quercoid."

Emended Diagnosis: Microphyll to Notophyll. Leaf shape elliptic, symmetrical, up to 12 cm long, 23-51 mm wide. Length to width ratio of 3:1. Apex acute; base acute and decurrent. Margin serrate, convex-convex teeth, nearly lobed. Petiole 9.5 mm long.

Venation of 5 orders, pinnate; secondary veins craspedodromous, alternate in origin, irregular spacing, vein angle of 45º originating and ultimately becoming 35º overall, originating every 5 to 7 mm. Tertiary veins random reticulate (approaching percurrent in places), acute from primary, 4th order veins regular polygonal reticulate. 5th order veins dichotomizing. Well developed areolation, 5 or more sided, free ending veins absent. Looped marginal ultimate venation. 3r organization. Teeth up to 7 mm wide, one order, straight straight to convex convex, angular sinuses, simple tooth apex. Texture not apparent.

Remarks: This species is rare in the overall flora, with a few possible leaves found in the typical *Glyptostrobus*/*Metasequoia*/*Zyziphoides*/*Platanus* swamps from localities US 817 and US 822. However, it is a common element of sub-flora 2 found at US 840. It is the most common angiosperm in sub-flora 2, and the 5th commonest element of this sub-flora, after *Mesocyparis borealis*, *Azolla schopfii*, *Corvirupestrobus adrielensis* and *Glyptostrobus dakotensis*. No cuticle has been recovered for these leaves, making association more difficult than it might otherwise be.

This species has only been identified in one previous report (Berry 1935). The type specimens are also from the Willow Bunch Lake map area. Berry distinguished this species on the basis of "less percurrent veins and less deeply cut margins" from *Quercus groenlandica* Heer (since transferred to *Fagopsiphyllum groenlandicum* (Heer) Manchester 1999). Specimens collected in the current study indicate the reticulation of the tertiary veins rarely approaches a percurrent orientation. In addition to the traits mentioned by Berry, a distinct tertiary vein larger than the rest but smaller than the secondaries runs to the sinus of each of the next tooth, which is not noted in the analysis of *F. groenlandicum*. The large teeth are also straight-straight to convex-convex, whereas the teeth of *F. groenlandicum* are largely concavo-convex. The angular sinuses of *F. praegroenlandicum* are also distinct from the commonly rounded sinuses of *F. groenlandicum*. The base is also acute and decurrent in the complete specimens, compared to the rounded bases known in *F. groenlandicum*.

The lack of reports of *Fagopsiphyllum praegroenlandicum* is likely due to later workers ignoring Berry 1935 and placing all specimens into *Fagopsiphyllum*

groenlandicum. There are many reports of *F. groenlandicum* in numerous Paleogene floras (Brown 1962; Boulter and Kvacek 1989), particularly those to the north of the Ravenscrag localities. In general outline, this species also resembles the leaves of *Fagopsis longifolia* (Lesquereux) Hollick from the Oligocene Florissant fossil beds (Manchester and Crane 1983). However, the details of the higher levels of venation differ, as does the presence of reproductive materials in *Fagopsis longifolia*.

Quercus groenlandica was transferred to *Fagopsis* by Wolfe (1977), as these leaves were likely in the family Fagaceae, but were not *Quercus* and were unassignable to any of the extant genera. Manchester and Crane (1983) published on *Fagopsis longifolia* from the Florissant fossil beds showing the attachment of fruiting bodies to what were considered *Fagopsis* leaves, but not of the generitype species. Therefore, a revision occurred, as *Fagopsis* is less than ideal for a morphogenus for isolated foliage, so the other species placed in *Fagopsis* without fruit need to be placed in another genus. *Quercophyllum* Koch has been utilized for isolated oak-like leaves, and was proposed by Koch (1963) for these purposes. However, the type specimen of *Quercophyllum* from the Cretaceous is not in the Fagaceae (Boulter and Kvacek 1989; Manchester 1999). Therefore, Manchester established *Fagopsiphyllum* in 1999 for these leaves, with what Heer called *Quercus groenlandica* as the type species for the genus. The addition of *F. praegroenlandica* amends the generic understanding slightly for *Fagopsiphyllum*. All of the other species have strictly percurrent venation, whereas *F. praegroenlandicum* adds the character of tertiary venation that is not percurrent.

Family Junglandaceae A. Richard ex Kunth
Genus: *Carya* Nutt.
Species: *Carya antiquorum* Newberry
Plate 14, figs. 1-4
Synonyms and References:
Carya antiquorum Newberry, 1868, p. 72; Newberry 1898, p. 35, pl. 31, figs. 1-2; Manchester 1987; Manchester 2001 fig. 5.
Localities: US 832 (US 817?)
Figured specimens: US832-9067, US832-9069, US832-9070, US832-9071

Description: Leaves suspected to be part of odd-pinnate compound leaves; however, all recovered specimens are singular unattached laminae. Laminae are elliptic, rarely ovate; symmetrical or asymmetrical, depending on leaflet. Apices acuminate; bases cuneate. Margins are serrate to entire and leaves are unlobed. Length longer than 150 mm, up to 62 mm wide. L:W ratios: 4.5:1, 3:1. Primary vein pattern is pinnate. Seconday veins are semicraspedodromous, with a uniform secondary angle of 45-55 degrees and uniform secondary spacing. No inter-secondary veins. Tertiary veins are opposite percurrent, with a straight to convex course, perpendicular to obtuse to the main axis, with the angle increasing exmedially. Quaternary veins are random reticulate with moderately developed areolation, which are 5 or more sided. Best classified as 3r. One order of tooth, 4 teeth per cm. Irregular tooth spacing. Tooth shape best described as straight/concave with rounded sinuses.

Remarks: This foliage is found primarily in locality US 832, where it is the most common element. Poorly preserved lanceolate leaflets with similar morphology are found in locality US 817, where they are rare elements. These leaves can be identified by their partially serrated margins, semicraspedodromous secondaries, long petioles, and that they are lanceolate leaflets. No complete compound leaves or reproductive materials were recovered. These specimens are suspected to be part of compound leaves due to variation of form between the leaflets (some are symmetrical and others are asymmetrical, which is common in odd-numbered compound leaves).

Familial assignment is somewhat in question, as these leaves may be *Aesculus hickeyi* Manchester (2001) (Sapindales) leaflets. Differences between Junglandaceous leaves and *Aesculus* L. leaves focuses on organization of the compound leaves (pinnate for the Junglandaceae vs. palmate for *Aesculus*) and a greater prominence of the tertiaries in Junglandaceae. The tertiaries are often weak in *Aesculus*, and may be missing even when present in other specimens from a given locality. However, the character of the tertiary vein preservation is a difficult trait, as it has only been utilized sparingly in the past, and is a relative character. No complete compound leaves have been found in this locality, so it cannot be determined if they are palmate or pinnately compound.

Higher orders of venation, including the tertiaries, are often poorly preserved in this locality, potentially leading to a misdiagnosis as *Aesculus hickeyi*. Tertiaries appear prominently on many specimens recovered. Combined with the palynology, these leaves are likely represent the Junglandaceae. However, this diagnosis is amongst the least definite in this study; further investigations will hopefully provide more complete compound leaves to increase confidence in the interpretations. It is clear that both of these plants were able to grow at these latitudes at that time, as specimens belonging to either *Carya antiquorum* or *A. hickeyi* have been recovered at other localities, including an *A. hickeyi* specimen from the Estevan map area (pl. 14, fig. 5).

It is strongly suspected that the generic assignment of *Carya* is incorrect for these plants (Manchester 2001). Instead, it is suspected that they are the leaves of an extinct member of the Junglandaceae. However, without reproductive materials, these specimens cannot be given a confident generic assignment, so this study follows the naming conventions across the Western Interior. The fossils from the Big Muddy Valley bear a similarity to the *Platycarya americana* Wing and Hickey foliar specimens (Manchester 1987) found in the late Paleocene Golden Valley collections as well as *Carya antiquorum* specimens from across the Western Interior. Palynological analysis shows no *Platycarya* Siebold et Zucc. pollen, but a wide variety of other junglandaceous pollen is present in the locality (Sweet 2007). *Platycarya* is not known to have evolved until the Eocene, based on both pollen and fruiting bodies (Wing and Hickey 1984), whereas palynological biostratigraphy places these localities in the earliest Late Paleocene (Sweet 2007). Therefore, these specimens are likely another Junglandaceous genus that merely resembles *Platycarya*.

Order Trochodendrales
Family Cercidiphyllaceae Engler
Genus: *Trochodendroides* Berry
Species: *Trochodendroides speciosa* (Ward) Berry
Plate 15, figs. 1-4
Synonyms and References:
Populus speciosa Ward, 1887, p. 20, pl. 5. figs. 4-7.

Trochodendroides speciosa (Ward) Berry, 1930, p. 22, pl 5, fig. 8; McIver and Basinger, 1993, p. 36, pl. 21, figs. 1, 2, 4 and all synonymies listed.

Localities: US 834, US 826 (US 822?, US 824?, US 830?)

Figured specimens: US826-9073, US822-9074, US834-9075, US834-9076

Description: Leaves ovate to elliptical mesophylls, 20-100 mm long, 12-100 mm wide with a 1-2:1 L:W ratio. Obtuse bases vary from rounded to often truncate. Obtuse apices are convex or rounded. Marginal petiole attachment. Actinodromous primaries and brochidodromous secondaries. Numerous agrophics from the lateral primaries. 3-7 basal veins, although always an odd number. Even vein spacing of the secondaries, typically 10-15mm, although the specimen that is 20 mm long has much closer spacing. Secondary veins arise at a 40 degree angle. Higher levels of venation are not visible due to poor preservation of all recovered specimens. Some specimens seem to have entire margins, but single serrate margins more common. The teeth are convex-convex.

Remarks: *Trochodendroides speciosa* leaves are found primarily in locality US 834, although individual leaves may be found in other localities, and are likely confused with *Archeampelos acerifolia* (Newberry) McIver and Basinger or *Zyziphoides flabella* (Newberry) Crane, Mancehster and Dilcher. Some poorly preserved leaves in US 822 likely respresent *Trochodendroides speciosa*, due to the presence of *Nyssidium arcticum* in this locality. However, leaves at US 822 more closely resemble *Z. flabella*. *Trochodendroides speciosa* can be best identified due to the combination of actinodromous primaries and brochidodromous secondaries with truncate bases compared to the cuneate base of *Z. flabella*, and the semicraspedodromous secondaries of *Archeampelos acerifolia*.

These leaves are ubiquitous in the Ravenscrag Butte flora (McIver and Basinger 1993), but are rarer in the Big Muddy flora. This likely reflects the same variation that led to the increased proliferation of *Glyptostrobus* in the Big Muddy Valley, especially compared to other localities. These specimens fit the diagnosis presented by McIver and Basinger (1993) for the most part, except for the smallest leaf, which has the minimum measurements for both length and width recorded in this study. This leaf is much more

elongate than the other leaves, skewing the length to width ratio. However, it bears the same teeth and general structures of the other leaves, so it is clearly part of this taxon.

The *Cercidiphyllum-Nyssidium-Joffrea* complex (Crane 1984; Crane and Stockey 1985) is commonly found in Paleogene floras of the Northern Hemisphere. It is typically assumed that this plant produced *Nyssidium* as its fruit, as *Nyssidium* resembles modern cercidiphyllous fruits. This association has been explored recently, with the realization that there is a complex system of associations of many closely related plants. Knowledge about this complex is best understood from materials collected from the Joffre Bridge Roadcut locality, Alberta, Canada (Crane and Stockey 1985). Remains in one layer included entire seedlings, greatly contributing to our overall understanding of this plant.

Numerous other leaves that resemble *Cercidiphyllum* Siebold et Zucc. from comparable localities have been placed in a wide variety of species over the years. A list of these is found in McIver and Basinger (1993). The relationships and divisions between these species are not well understood. A cautious and precise definition was adopted in the circumscription of *Trochodendroides speciosa*, so these and later specimens, such as those reported in Johnston (2002) and Barclay et al. (2003), are not included in the synonymy list. Barclay et al. (2003) consider *Trochodendroides speciosa* to be part of their understanding of *Cercidiphyllum genetrix* (Newberry) Hickey. However, given that McIver and Basinger (1993) considered the types and material of Hickey in their assessment, and there is no accompanying discussion explaining why Barclay et al. (2003) reject the claims of McIver and Basinger (1993), it is reasonable to ignore this lumping. Specimens collected by Barclay et al. (2003) are largely unillustrated, so it is impossible to assess if any of their *C. genetrix* materials should be placed in *T. speciosa*.

Genus: *Nyssidium* Heer

Species: *Nyssidium arcticum* (Heer) Iljinskaja

Plate 15, figs. 5-6

Synonyms and References:

Nyssa arctica Heer, 1869, p. 477, pl. 43, fig. 12c, pl. 50, figs. 5-7.

Nyssidum arcticum (Heer) Iljinskaja, 1974, p. 124, pl. 53, figs. 9-13; Crane et al., 1990, p. 13, fig. 10 d-g; McIver and Basinger, 1993, p. 37, pl. 20, figs. 5,6, pl. 21, fig. 3, pl. 22, figs. 1-3, and all synonymies listed.

Localities: US 834, US 822, US 841 (US 820?, US 817?, US 840? US 830?)

Figured specimens: US932-9077, US834-9078

Description: Fruit occurs in racemose inflorescences. One major abscission scar often visible. Typically ellipsoid, although usually bearing at least some compression, 6 mm wide, 11mm long.

Remarks: Shed fruit occur both singularly and in infructescences throughout the study area. Localities US 834 and US 841 show the greatest abundance of these fruit. US 822 has many preserved as impressions. The other localities contain only single occurrences of these fruits.

Nyssidium arcticum is a common element of Paleogene forests of this type (Brown 1962). Association shows that these fruits are part of a plant complex referred to as the *Nyssidium-Joffrea-Cercidiphyllum* complex, which is a difficult taxonomic problem (Crane and Stockey 1985). There are multiple morphologies of all of these organs, and associations between the various morphologies of the organs can be drawn, so that any leaf can be found with multiple types of fruit, both of which can be found with multiple types of staminate organ.

There are a number of variations to the morphologies of *Nyssidum arcticum* inflorescences recorded from other localities (McIver and Basinger 1993). The majority of *N. arcticum* specimens collected from the area are found isolated, shed from their inflorescences. However, a few inflorescences have been recovered from the region. Shed fruit occur both singly and in abundance throughout the study area. Localities US 834 and US 841 show the greatest abundance of these fruits. US 822 has many preserved in impression. The other localities contain only single occurrences of these fruits.

Typically, these fruits are considered to be the fruit of a cercidiphyllous element of these floras. However, the variation in inflorescence morphology shows that this species of fruit is not a good biological species, but instead a morphospecies accounting

for elements of many biological species. They remain in one species as the variation in inflorescence is often obscured by the shedding of these fruits in the rock record. Additionally, few of the inflorescences have been found attached to leaves, and even those that have been found do not imply exclusive attachment between these two organ morphologies. Other combinations are likely to occur as well, as potentially separate species.

There is some question whether these specimens would be better placed in *Cercidiphyllum* per Crane and Stockey (1985). McIver and Basinger (1993) used *Nyssidium* as they noticed that their specimens had dehiscence on the opposite side as the specimens of Crane and Stockey. Unfortunately, the specimens from this study do not show either. However, the specimens closely resemble those of McIver and Basinger (1993). Given that complete inflorescences recovered from the Big Muddy Valley in 1992 were amongst specimens considered in the monograph on the Ravenscrag Flora, these more poorly preserved specimens should follow suit.

Family Trochodendraceae Eichler

Genus: *Zyziphoides* Seward and Conway

Species: *Zyziphoides flabella* (Newberry) Crane, Manchester and Dilcher.

Plate 16, figs. 1-3, 5

Synonyms and References:

Populus flabellum Newberry 1868.

Zyziphoides flabella (Newberry) Crane et. al. 1991, and all synonymies listed; Johnson, 2002; Barclay et al., 2003.

Trochodendroides flabella (Newberry) McIver and Basinger, 1993.

Localities: US 821, US 822, US 823, US 830 (US 817?, US 826?, US 828?)

Figured specimens: US822-9079, US830-9080, US822-9081, US822-9083

Description: Ovate to elliptic symmetrical mesophylls. 30-80 mm long, 20-73 mm wide, L:W ratio 0.8-1.5:1. Obtuse bases and obtuse apices. Bases are convex, ranging from rounded to truncate with marginal petiole attachment. Apices are convex or rounded. Actinodromous primary veins and brochidodromous secondary veins, usually with compound agrophics. 3-7 basal veins, always showing an odd number. Higher

order vein orders were not preserved on recovered specimens. Usually entire margins, but single serrate margins sometimes occur.

Remarks: *Zyziphoides flabella* leaves have been recovered from US 817?, US 821, US 822, US 823, US 826?, US 828?, US 830. They are identifiable due to actinodromous primary veins and brochidodromous secondary veins. The localities with question marks yielded ambiguous specimens, which may be specimens of *Archeampelos acerifolia*, the cordate based leaves of US 828, *Joffrea speirsii* Crane and Stockey or *Trochodendroides speciosa*, all of which exhibit the actinodromous primaries and some brochidodromous nature to their secondaries. In general, *Zyziphoides* can be most easily recognized by its typically cuneate base, compared to rounded bases of *T. speciosa*. It is abundant and a common element of the swamp floras, both in the Big Muddy Valley and in many localities across the Western Interior and Northern Hemisphere, though due to vagaries of naming and the difficulty of distinguishing from the other "trochodendroid" leaves, which part of the diversity is shown in the four species above, makes it hard to tell exact distribution. However, it has been reported from many Fort Union Sites and Ravenscrag Butte (Johnson 2002; McIver and Basinger 1993; Pigg et al. 2007).

As seen in the synonomy list, this taxon has undergone extensive revision recently. An association of these leaves and *Nordenskioldia borealis* fruit has led to a consideration that these belong to the same plant (Crane et al. 1991), but no attached specimens have been recovered. However, the association is consistent, so it seems likely that these are from the same plant. *Nordenskioldia borealis* fruit were not found at Ravenscrag Butte. However, specimens were found in the two localities that produced the most *Zyziphoides flabella* specimens in this study.

The generic name is contested, although the majority of workers seem to prefer *Zyziphoides*, as they feel the name *Trochodendroides* implies too close of a taxonomic affinity between these leaves and *Trochodendron* Siebold et Zucc., as well as the fact that *Trochodendrondroides* is a form genus with unclear affinities, or possibly mixed affinities. As shown by the two *Trochodendroides* species named by McIver and Basinger (1993), currently considered as species of *Zyziphoides* and *Cercidiphyllum* in the work of Johnson (1989) and Barclay et al. (2003) these plants can be distantly

related but still placed in this genus due to morphological similarity. Unlike other species that have been placed into *Trochodendroides*, *Zyziphoides* does show clear association with *Trochodendron* (Crane et al. 1991), as they both have vessel-less wood in their short shoots, and *Nordenskioldia* fruit resemble *Trochodendron* fruit.

Genus: *Nordenskioldia* Heer
Species: *Nordenskioldia borealis* Heer
Plate 16, figs. 4,6; pl. 17, fig. 1
Synonyms and References:
Nordenskioldia borealis Heer, 1871, p. 65, pl. 7, figs. 1-13; Brown, 1962, p. 89, pl. 67, figs. 13, 45; Crane et al., 1991, and all synonymies listed.
Localities: US 830, US 822 (US 828?)
Figured specimens: US830-9082, US830-9084, US830-9085
Description: Fruits found isolated or sometimes attached to shoots. Borne in opposite pairs along shoots when attached. Globose fruit composed of approximately 15 follicles, 8 mm to 15 mm in diameter. Follicles are often loosely articulated, often appearing with distinct separating gaps. Both transverse and lateral sections recovered, which appear distinct, with lateral sections appearing as many parallel, individual structures and transverse appearing as round structures.

Remarks: This plant is common in one locality, US 830, with rare specimens occurring throughout the sub-flora 1 localities, where they are often poorly preserved. There is a common association with *Zyziphoides flabella* leaves, *Nyssidium arcticum*, *Cercidiphyllum genetrix* (Newberry) Hickey leaves, *Glyptostrobus dakotensis* and *Metasequoia occidentalis*. Its abundance is proportional to the presence of the angiosperms in this sub-flora. Where the localities are conifer-dominated, these fruits are rare. The variation between the localities is likely due to slight variations in the depositional environments. This is supported by the presence of large roots within these beds, which are absent in the conifer-dominated beds.

These fruits are considered to be the fossil fruit of a member of the Trochodendraceae due to the lack of vessels in the wood and overall similarity with the

fruit of *Trochodendron* (Crane et al 1990; Crane et al. 1991; Pigg et al. 2007). *Nordenskioldia borealis* was a common element of Paleogene forests of North America and the Arctic. It is commonly associated with *Zyziphoides flabella* leaves, and it is thought that these are the leaves of this plant (Manchester et al. 1991). However, this link is sufficiently spurious that uniting them is not practical. Additionally, keeping these leaves and fruits separate allows for the variation of pairing of leaves with fruits, so variant fruits can be found with *Zyziphoides*-type leaves as well. Many plants bear leaves of that form.

These fruits are variable in appearance, leading to difficulties in identification, as the various specimens do not closely resemble one another. However, the variation expressed in the population seems to be consistent throughout its range, likely representing variations in orientation and maturity of the specimens.

Order and Family: Incertae Saedis
Genus: *Archeampelos* (Newberry) McIver and Basinger
Species: *Archeampelos acerifolia* (Newberry) McIver and Basinger
Plate 17, figs. 2-4
Synonyms and References:
Ampelopsis acerifolia Newberry, 1868.
Archeampelos acerifolia (Newberry) McIver and Basinger, 1993, and all synonymies listed.
"Populus" nebrascensis Lesquereux *sensu* Johnson, 2002, (FU7); Barclay et al., 2003, (BC 37).
Localities: US 817, US 821, US 822, US 823, US 828, US 834, US 838
Figured specimens: US817-9086, US817-9087, US817-9088, US817-9088
Description: Obovate, small mesophylls with symmetrical lamina. L:W ratio 1:1; 5-8 cm wide and 6-8 cm long. Obtuse bases and obtuse apices. Leaf bases are convex, rounded or truncate, with marginal petiolar insertion, and the apices are convex. Serrate to crenate margins, and exhibit no lobing to their architecture. 3 or 5 primary veins, with 5 being more common. Veins basally actinodromous. Secondary veins are craspedodromous to semicraspedodromous with compound agrophics. Besides the 3 or

5 primary veins, there are a number of other veins that orginate at the base, so that leaves exhibit 7-9 basal veins. Secondary veins are irregularly spaced, with the vein angle smoothly increasing towards the base. Leaves lack inter-secondary veins. Tertiary veins best described as opposite, convex percurrent, although they are rarely alternate, convex percurrent, which are acute to the primaries, with this angle increasing exmedially. Quaternary veins are oppostite to alternate percurrent. Fifth vein order is regular polygonal reticulate, with well developed areolation. Free ending veins are absent. 6 orders of veins are noted on these leaves, with secondaries likely being the highest excurrent veins. Marginal venation is looped. Leaves are organized to 4r. One order of teeth, with 1-2 teeth/cm with regular spacing. Teeth convex/convex type with rounded sinuses and simple tooth apices. Texture coriaceous without cuticle preserved.

Remarks: Specimens of this plant occur commonly throughout the beds with the first sub-flora. This is amongst the commonest angiosperms recovered in region. Complete, or near complete, specimens have been recovered from many localities, particularly US 817. Isolated bases of these leaves can be difficult to distinguish from the cercidiphyllids, so caution is advised in identifying these remains. However, the distal margins are readily identifiable due to the marginal termination of the lateral primaries, instead of arching back towards the centre vein.

The taxonomy of these leaves has been debated recently, with no resolution (McIver and Basinger 1993; Johnson 2002; Barclay et al. 2003). Those workers concerned with climate resolution through the application of morphotypes have taken to using the obviously incorrect "*Populus*" *nebrascensis* for this plant (Johnson 2002; Barclay et al. 2003). They disregard the suggestions of Brown (1962), Chandrasekharam (1974) and McIver and Basiger (1993) about taxonomic affinity of these leaves. The climate resolution/morphotype workers have also proposed an affinity with the Cercidiphyllaceae (Johnson 2002; Barclay et al. 2003). The rejection of the numerous names associated with the Vitaceae seems to stem from this, but it is not explicitly stated. No reproductive organs have been found linked to these leaves, either directly or by statistical association, so either of the familial placements can only be considered speculative, and no clear solution can be elucidated from these remains.

However, familial placement has no bearing on the use of the genus *Archeampelos* for these plants,

Due to placement within the Vitaceae by some workers in the past, there has been the proposal that these leaves represent remains of lianas (McIver and Basinger 1993); however, the leaves of this study were found as isolated specimens with no additional evidence for this growth. Other than possibly *Lygodium* sp., none of the other plants have a suspected liana growth form.

Subclass Rosidae
Order Cornales
Family Cornaceae Dumotier
Genus: *Cornophyllum* Newberry
Species: *Cornophyllum newberryi* (Hollick) McIver and Basinger
Plate 19, figs. 2-3
Synonyms and References:
Cornus newberryi Hollick, Newberry, 1898, Geol Surv. Mon. (US) 35, p. 124, pl. 37, figs. 2-4.
Cornophyllum newberryi (Hollick) McIver and Basinger, 1993, p. 45, pl. 35, figs. 2-5, pl. 36, figs. 1-3 and all synonymies listed; Johnson, 2002, pl. 17, fig. 4; Barclay et al., 2003, fig. 11 D.
Localities: US 817, US 822, US 843, 1992 collections
Figured specimens: US822-9094, US817-9095
Description: Microphylls, perhaps small notophylls for some of the small ones with ovate lamina. Symmetrical and asymmetrical bases. 55-66 mm long, 20-44 mm wide; L:W ratio 3:1. Acute base angle and acute apex angle. Cunneate to convex bases with marginal petiolar attachment. Petioles at least 22 mm long. Straight apex. Margins serrate, leaves unlobed. Primary veins pinnate. Secondary veins craspedodromous, although they approach weak brochidodromous. No agrophics. One primary and two tertiary basal veins. Uniform secondary vein spacing, and uniform secondary vein angles (acute, ~30 degrees). Weak intersecondary veins. Tertiary veins are random reticulate, sometimes approaching alternate percurrent. Acute tertiary to primary vein

angle, although it is inconsistent. Quaternary veins are regular reticulate with moderately developed areolation. Marginal veins have incomplete loops. 3r organization. 3 orders of teeth, with irregular spacing, best described as concavo-convex with angular sinuses. Simple tooth apices, with only the principle vein entering. Specimens have no preserved cuticle.

Remarks: *Cornophyllum newberryi* is a rare element found in many of the similarly-aged floras. Few specimens have been recovered from the Big Muddy Valley, only from the diverse lowland swamp floras. Specimens are identifiable by their distinctive venation, which resembles that of extant *Cornus* L. The leaves exhibit a wide range of variability.

This plant occurs in sub-flora 1 exclusively, which is consistent with findings from other similarly-aged floras, which commonly see an association between this plant and the common elements of the swamp sub-flora (McIver and Basinger 1993). This plant was transferred to the genus *Cornophyllum* because there are sometimes teeth present, as is the case with specimen US 817-1, which are absent in the extant *Cornus*. However, some specimens do not have these teeth, instead having entire margins like extant *Cornus* (Barclay et al. 2003). No reproductive materials are known for this plant (McIver and Basinger 1993), which makes the case for placing these specimens into *Cornophyllum* stronger, because even though they do resemble *Cornus* in many characters they differ or are ambiguous in others.

Specimens recovered from the Big Muddy Valley are typical of this species, and do not deviate in their characters from the diagnosis. Many of these specimens are largely incomplete. However, in one specimen a complete leaf is preserved. This leaf includes more of the petiole than illustrated by McIver and Basinger (1993). However, petioles being preserved is not uncommon for this genus, and the petioles in McIver and Basinger (1993) seem truncated not by natural abscission, but by physical means, being obscured by other plant materials or crossing the margin of the rocks.

Family Nyssaceae Dumortier

Genus: *Browniea* Manchester and Hickey

Species: *Browniea serrata* (Newberry) Manchester and Hickey 2007

Plate 4, fig. 3; Plate 18, figs. 1-4; Plate 19 fig. 1

Synonyms and References:

Alnus serrata Newberry, 1868, p. 55; Newberry, 1898, p. 66, pl. 33, fig. 11 (Holotype).

"Eucommia" serrata (Newberry) Brown, 1962, p. 72.

Tapiscia serrata (Newberry) Chandrasekharam, 1974, p. 29, pl. 21, figs. 136–138.

Dicotylophyllum anomalum (Ward) Hickey, 1977, p. 147; McIver and Basinger, 1993, p. 51–53.

Amelanchites similis (Newberry) McIver and Basinger, 1993, p. 42.

Browniea serrata (Newberry) Manchester and Hickey 2007 p. 231 and all synonymies listed.

Localities: US 817 US 822, US 830, US 838, US 840

Figured specimens: US817-9023, US840-9089, US830-9090, US840-9091, US830-9092, US817-9093

Description: Leaves are small mesophylls in size, with elliptic, asymmetrical simple lamina. Obtuse basal angles and convex bases. Apices are acute. Marginal petiolar attachment. Partial petioles are preserved in a few specimens, the longest being 9 mm long. Serrate margins, and are unlobed. L:W ratio 1.8:1, up to 12 cm long, 7 cm wide. Smaller leaves also common, with many specimens 5 cm long, but total length enigmatic as they lack the apices. Pinnate primary veins with compound agrophics, and 3 basal veins. Secondary veins are craspedromous to semicraspedromous with uniform spacing, although some specimens show slight irregularities to the spacing, so that the secondary veins arise oppositely at the base, but are staggered distally in the laminae. Secondary veins have a uniform secondary angle. Inter-secondary veins are absent. Tertiary veins are mixed opposite and alternate percurrent in form, and are obtuse to the primary vein. The quaternary veins are reticulate with moderate areolation. One order of tooth, frequency of 2.5 per cm. The tooth shape is a convex/concave type with rounded sinuses and simple tooth apices. One isolated fruit recovered, 4 mm wide, 11 mm long with 3 visible carpels, 1mm long terminal lobes.

Remarks: Specimens are found primarily from locality US 830, where they appear with some frequency. They are also found in locality US 840 where they are rare, but are one of only two angiosperms recovered. In localities US 838 and US 822, they are rare, and although numerically similar in abundance to US 840, they seem rarer due to a more extensive angiosperm record. A single fruit appearing similar to those presented in Manchester and Hickey (2007) was found in locality US 817 (pl. 19 fig. 1).

This species is commonly found across the Paleocene Great Plains paleofloras. It is not considered a dominant element, but instead a typical supporting element. It is a relatively rare element of the present localities, and is only found in the swamp sub-flora. This paucity of specimens is notable, and likely reflects a slight variation in environmental characters in the area compared to other Paleocene localities in the Western Interior.

Recently this species was established from many disparate taxa (Manchester and Hickey 2007), and placed in the Nyssaceae. A single fruit was found with no association with the leaves in this study. It exhibits the calyx lobes mentioned in the diagnosis of both the genus and species of this plant. However, this fruit is slightly smaller than those recorded in Manchester and Hickey 2007, and has a slightly more pointed proximal end. These differing traits seem sufficiently minor to include this single specimen in this species. Should more specimens appear consistently within this new size range, especially if they are part of complete infructescences or closely associated with *Browniea serrata* foliage, it may be worth re-examining the diagnosis.

Leaves of *Browneia* found around the Big Muddy Valley exhibit numerous fine serrations, compared to many of the figured specimens which have fewer and larger teeth (Manchester and Hickey 2007). However, the fine serrations are well within the natural range expressed by the taxon (Fig. 9A Manchester and Hickey 2007). The leaves recovered in these localities include both asymmetrical and symmetrical leaves. There is notabe variation present in the potential morphologies of *Browniea* leaves, as explained in the recent revision. These specimens only exhibit part of this variation, although they are diverse enough that there was some difficulty in recognizing the similarities between these specimens. From the synonymy list, the Big Muddy Valley specimens closely resemble those specimens assigned to *Tapiscia serrata* from the

Genesee locality (Chrandrasekharam 1974), sharing the same bases and teeth. This difficulty has also appeared in other studies of the Ravenscrag Formation, as Hickey and Manchester (2007) included both *Amelanchites similis* and *Dicotylophyllum anomalum* from McIver and Basinger (1993).

Genus: *Davidia* Baillon
Species: *Davidia antiqua* (Newberry) Manchester 2002
Plate 19, fig. 4
Synonyms and References:
Tilia antiqua Newberry, 1868.
Viburnum antiquum (Newberry) Hollick, 1898.
Davidia antiqua (Newberry) Manchester, S.R., 2002, and all synonymies listed.
Localities: US 820, US 822
Figured specimen: US820-9096
Description: Leaves are notophylls or mesophylls, 40-60 mm wide, unknown length, at least 65 mm. Symmetrical ovate laminae. Obtuse base angles and acute apex angles. Bases are convex or rounded with marginal petiolar insertion. Apices are straight. Leaves are unlobed. Primary veins are pinnate, but may appear palinactinodromous due to extensive agrophics. Secondary veins are craspedodromous. Numerous simple agrophics. Uniform secondary vein spacing, uniform secondary vein angles. Inter-secondary veins are absent. Tertiary veins opposite percurrent. One order of teeth, which appear with a frequency of 2 per cm, with irregular spacing. Teeth best described as straight straight with angular sinuses and simple tooth apices.

Remarks: These leaves are a minor member of the *Glyptostrobus* dominated swamp environment. Only US 820 and US 822 have produced clearly identifiable specimens, but it is likely that more sampling of the other back-swamp localities would produce them, given the similarities between these localities. These leaves are found in fine-grained shales associated with these flooded swamps.

These leaves are distinguishable by their agrophics, which are simple and arise from the lowest pair of secondary veins alone. They most closely resemble the

Ettingshausenia leaves in the area, due to the basal secondaries resembling a palinactinodromous veins. However, they differ due to their smaller size and ovate outline, which gives no inidication of the lobing of the leaves in *Ettingshausenia*. None of these leaves have the extended concavo-convex bases present on many of the *Ettingshausenia* specimens found both in this area, and in other Paleocene localities (Boulter and Kvacek 1989; Kvacek et al. 2001).

Manchester (2002) transferred leaves of this type to *Davidia antiqua* (part of the Nyssaceae) due primarily to a strong association of these leaves with fruit that showed that they were part of *Davidia*. This association is one of many recently, where Paleocene specimens originally placed in *Viburnum* L. have been revised and placed in genera in the Nyssaceae. The characters that distinguish the leaf taxa from one another in this group are said primarily to be the ratio of the length of the petiole to the lamina, and the nature of the margins. Unfortunately, the specimens recovered do not preserve petioles. However, their strictly craspedodromous venation, acute tips, rounded bases, rather pectinate organization and blunt, irregular teeth all fit with the description of *Davidia antiqua* leaves.

Order and Family: Incertae Saedis
Genus: *Quereuxia* Kryshtofovich
Species: *Quereuxia angulata* (Newberry) Kryshtofovich
Plate 20, figs. 2-3
Synonyms and References:
Neuropteris angulata Newberry, 1861, pl. 3, fig. 5.
Trapa angulata (Newberry) Brown, 1962, and all synonymies listed.
Trapago angulata (Newberry) McIver and Basinger, 1993, and all synonymies listed; Hoffman and Stockey, 1997.
Quereuxia angulata (Newberry) Kryshtofovich, 1953; Hickey, 2001, and all synonymies listed.
Localities: US 817, US 820, US 845 (US 822?)
Figured specimens: US845-9098, US845-9099

Description: Compound leaves, part of a large rosette in the most complete specimens. Most specimens paired or solitary leaflets. Leaflets on dichotomously branching petioles. Leaflets are symmetrical obovate notophylls, 7mm wide, up to 15 mm long. Base and apex rounded. Venation is dichotomizing. Compound serrate margins, especially across the distal margin.

Remarks: This is a rare element of the sub-flora 1, represented by only a few specimens. However, it is a common element at US 845, which is composed of 3 similarly abundant elements: *Quereuxia angulata*, *Paranymphaea crassifolia* and *Azolla vellus*.

This plant is common in many of the Paleocene floras of the Great Plains, and is particularly common in many beds in the Cypress Lake map area (E.E. McIver, personal communication 1995). Its relative rarity in the Big Muddy Valley may be due to a slight variation in depositional environment, likely reflecting the widespread *Glyptostrobus* swamps comprising the environment of the Big Muddy Valley near highway 34.

This plant was variously called *Trapa* or *Trapago* due to superficial resemblance of foliage to the extant genus *Trapa*. However, there is little to support a close relationship between these fossil specimens and living *Trapa*. It is questionable whether the similarity in bauplan is reflective of convergence or phylogenetic affinity. Instead, these plants are placed in the genus *Quereuxia*, named for Russian materials (Hickey 2001). This assignment follows the general trend, despite arguments against this generic name made by McIver and Basinger (1993). They felt that the type specimens of *Quereuxia* presented by Krystovovich did not reflect the materials they had found. However, modern taxonomic lists follow the advice of Hickey (2001), which for clarity is followed here as well. Specimens from the Big Muddy Valley contribute to a resolution of the taxonomic difficulties.

Family: Incertae Saedis

Genus: *Harmsvernia* gen. nov. ≡ *Harmsia* McIver and Basinger (1993: 54).

The genus *Harmsia* McIver and Basinger 1993 was established for an aquatic species of angiosperm of unknown familial affinity from the Paleocene of the Western Interior

Basin of North America. The one species, *Harmsia hydrocotyloidea* McIver and Basinger, was based only on foliage of the plant, as the reproductive organs are unknown (McIver and Basinger 1993). The etymology of the generic name was in honour of Dr. Vernon L. Harms, curator of the W.P. Fraser Herbarium in the University of Saskatchewan from 1969 to 2000. Further investigation shows, however, that *Harmsia* K. Schum. holds priority for this name. Therefore, as per Article 53.1 of the International Code of Botanical Nomenclature (Vienna Code) (2006), *Harmsia* McIver and Basinger is illegitimate and must be rejected. *Harmsvernia* nom. nov. is proposed as a replacement generic name, following the same etymology, which is to honour Dr. Vernon Harms.

Species: *Harmsvernia hydrocotyloidea* (McIver and Basinger) comb. nov.
Plate 20, fig. 1.
Synonyms and References:
Harmsia hydrocotyloidea McIver and Basinger, 1993, p. 54, pl. 45, figs. 1-3, pl. 46, fig. 1; Johnson, 2002, pl. 15, fig. 3.
Type: UAPC-ALTA S8029, Paskapoo Formation, Alberta (McIver and Basinger 1993, pl. 45, fig. 1)
Localities: US 826
Figured specimen: US826-9097
Description: Small macrophylls, elliptic lamina, symmetrical, 1:1 ratio length to width, up to 20 cm diameter. Circular basal angle, peltate central petiolar attachment, unlobed, 8 major veins, each giving off secondaries from both sides, arising at about 45 degree angles.

Remarks: Only one specimen and its counterpart were found in locality US 826, and these were poorly preserved. It is identifiable by its radiating central venation with 8 major veins. Unfortunately the margin of the specimen is not preserved; therefore, the distinctive terminal glands are not visible. Due to its larger size, this may represent a different species or genus. However, due to the limited specimens known of this

species, as well as the overall similarity of venation, this specimen is placed into *Harmsvernia hydrocotyloidea*, resulting in a broader understanding of this species.

Harmsvernia hydrocotyloidea seems to have been a rare plant, contributing to its late identification in floral studies of the Great Plains. Given that it appears to be a floating aquatic, its scarcity likely reflects actual distribution in localities, and not the addition of a common floral element from a less preserved floral type, such as from mesic environments. All records of this plant include it as a rare member of the flora (McIver and Basinger 1993, Johnson 2002).

Reproductive structures of this plant are unknown, making higher-level taxonomic placement speculative at best. The rarity of this plant makes this find useful for the overall understanding of this plant, despite the poor preservation and limited numbers.

Unknown angiosperm 1
Plate 21, fig. 1
Localities: US 822
Figured specimen: US822-9100
Description: Structure, which may be an angiosperm fruit, infructescence, inflorescence or a conifer cone (which would possibly make it an unknown conifer instead). 10 mm wide, 7 mm long. Structure terminal on a 1 mm wide stalk. At least 6 walls, which may be a number of structures including fruit walls or bract-scale complexes. At least 3 of the areas between the walls contain potential reproductive materials, possibly seeds or fruit. Walls appear to be plicated structures, made of many thin sheets.

Remarks: This specimen was recovered from locality US 822, from one of the impression beds slightly above the *Nelumbago* deposits. A single impression of a reproductive body of a seed plant. However, it is unclear whether it is a reduced, heavily bracted cone like *Cunninghamia* or an inflorescence of the same general form. Finding additional specimens that are not just impressions would facilitate this process greatly, but will likely require other localities to do so, as this specimen is from the impression fruit bed of US 822, which is found slightly above the *Nelumbago* bed.

Nyssidium arcticum and *Nordenskioldia borealis* as well as a *Corvirupestrobus adrielensis* were also recovered from this bed, all exhibiting the same preservation.

Unknown angiosperm 2
Plate 21, figs. 2-3
Localities: US 828
Figured specimens: US828-9101, US828-9102
Description: 5 (10?) loculed globose fruit, 8-10 mm in diameter and length.

Remarks: Two isolated fruit found on one bedding plane of US 828, one in transverse section, one in longitudinal section. Unclear taxonomic affiliation. Unfortunately, no anatomy is known of these fruit, making identification difficult, although based on the 5 fold symmetry, they are non-monocot angiosperms of some form, likely within the Eudicots. Additional specimens are required for definitive placement. It is possible that these are the fruits of the unknown cordate leaves. However, as few specimens of either have been recovered, this diagnosis is spurious. The only angiosperm leaves common in this locality are platanoids and trochodendroids. The fruit do not correspond to either.

Unknown angiosperm 3
Plate 21, fig. 4
Localities: US 836
Figured specimen: US836-9103
Description: Specimen is about about one half of a leaf from the middle portion. Leaves are notophylls, with elliptic assymetrical lamina, at least 65 mm wide and over 80 mm long. Base angle is obtuse. Apices likely obtuse, although the specimen is incomplete so this is not clear. Base and apex shapes are unknown. Leaves have entire margins and unlobed. Pinnate primary veins. Secondary veins are weak brochidodromous, with no visible agrophics. It appears that there is one basal vein, but as the base is missing, it is impossible to tell. Secondary veins spacing is irregular, but secondary angle is uniform. Inter-secondary veins are present in these leaves. Tertiary veins are straight, opposite percurrent, with an obtuse angle to the primary that decreases

exmedially. Quaternary veins are opposite percurrent with well developed areolation. Leaf organization is 4r. Leaf texture is coriaceous.

Remarks: Only one specimen recovered from US 836. Unfortunately this leaf is missing both the tip and base. However, they are inferred as only the direct base and tip are missing. The leaf is reconstructed as thick, with thicker veins than other leaves found in this study. It was recovered in a bed with overall poor compression preservation, dominated by *Glyptostrobus*, although many of the specimens do not exhibit the needles clearly. All other recovered remains from US 836 were recovered in smaller blocks than this leaf, so additional specimens are better sought at other localities.

Unknown angiosperm 4
Plate 21, fig. 5
Localities: US 822
Figured specimen: US822-9104
Description: Suspected to be a portion of a much larger leaf. Visible portion is 58 mm wide, 66 mm long. No central vein recovered. Base appears cordate. At least 3 basal veins per side, all sharply curving to a single point. Vein angle varies greatly. Leaf with at least 3 lobes. First lobe formed by the second vein. All of the basal veins produce secondary veins only towards the margin. First and second basal veins give rise to one secondary, third basal vein gives rise to at least 2 more. Margin is simple serrate. Lamina thin.

Remarks: Only one partial specimen recovered from US 822, about 1 m above the shelf on the valley wall. Found on a rock with other angiosperm species, including *Zyziphoides*. The specimen is incomplete, found at the edge of the rock. It resembles no other specimens from the Big Muddy Valley.

Architecture of the leaf is interpreted as symmetrical, due to the presence of all veins curving from a single point, assumed to be the point of petiolar attachment. These assumptions are supported by the distribution of veins, which all appear on the marginal

side of each of the visible veins, which is typical for lobed leaves with multiple basal veins.

The preservation of this leaf does not include tertiaries, and is incomplete, thereby rendering affinity impossible to determine. The steeply arching third basal vein is not present in any other known specimen.

Unknown angiosperm 5
Plate 21, fig. 6
Localities: US 845
Figured specimen: US845-9105
Description: 4 lobed structure, lobes in an elongate ”X”. 16 mm long, 8 mm wide. Small central cross-shaped structure, 1.5 mm long, 1.2 mm wide, with the points facing the junctions of the elongate “X”.

Remarks: One specimen found in the floating aquatic bed US 845. This structure possesses the proper radial symmetry to be a flower, although the preservation is not sufficient to determine this diagnosis. It is unattached, so its affinity is unclear. However, if it is *in situ*, then it likely would be a flower of one of the angiosperms in this bed. Only *Quereuxia angulata* and *Paranymphaea crassifolia* were recovred from this bed. It is possible that this is the flower of one of these two plants, neither of which has known reproductive structures or clear affinity with any of the angiosperm families. McIver and Basinger (1993) had fruit associated with *Quereuxia angulata*, but these were disputed and have since been shown to be *Browneia serrulata* fruit (Manchester and Hickey 2007).

Unknown angiosperm 6
Plate 22 fig. 1
Localities: US 828
Figured specimen: US828-9106
Description: Oblong mesophylls, with symmetrical laminae. Incomplete leaves at least 86 mm wide, at least 100 mm long. L:W ratio unknown, as apices are lacking. Base

angle is obtuse, lobate base with marginal petiolar attachment. Apex is unknown. Serrate margins. Known portions of the laminae are unlobed. Actinodromous primary veins with 5 at least basal veins and compound agrophics. Secondary veins are craspedodromous or possibly semicraspedodromous. Secondary vein spacing decreases towards the base, while secondary vein angle smoothly increases towards the base. Inter-secondary veins are absent. Tertiary veins are opposite percurrent, convex, and range from parallel to obtuse to the primary veins, with the angle increasing exmedially. Veins form incomplete loops marginally. Teeth concave/convex, with at least 2 orders of teeth, irregular spacing, and rounded sinuses.

Remarks: Found in locality US 828. One specimen is the primary designator of this material, although other leaves may be this taxon as well. This leaf has a general "*Trochodendroides*" architecture, with prominent actinodromous primary venation. However, it has distinct compound serrated margin and a lobate base that are different from other leaves found in this study.

There are many varieties of actinodromous leaves of this type found in Late Cretaceous and Neogene floras, which have been placed in many taxa. It can be difficult to distinguish these taxa from one another (Pigg et al. 2007). Of these taxa, these leaves show the most similarity to *Tetracentron* Oliv. (Pigg et al. 2007). The specimen is too fragmentary to make proper assessments. However, following the advice presented in their review, it is best to not place this specimen in *Tetracentron*, rather than clutter up this genus with poorly understood specimens that would increase confusion in an already confusing taxonomic scheme. Additionally, these teeth do not share the consistent size recorded in any of the taxa. Only *Zyziphoides* has irregular teeth; however, its teeth are much larger and more rounded. This plant also has craspedodromous or semicraspedodromous secondaries, something that *Tetracentron* and *Cercidiphyllum* approach, but that *Zyziphoides* never does (Pigg et al. 2007).

Another leaf with actinodromous primaries and a cordate base was recovered from the area in 1992 and is stored in the USP collections (pl. 22, fig. 2). Its taxonomy is also not determined. It differs from the specimen in this study in a number of traits. First, it has entire margins instead of the serrated margins present in the US 828

specimen. Secondly, it has well developed brochidodromous venation in the secondaries, on the edge of festooned brochidodromous venation, which is distinct from the camptodromous or semicamptodromous venation seen in the US 828 specimen. However, they share similarities in shape, size and appearance of the primaries. These specimens illustrate the need for caution when dealing with fragments of the wide variety of plants that existed during the Paleogene.

CHAPTER 6
DISCUSSION

6.1 Sedimentological and Environmental Interpretations

6.1.1 Sedimentology

6.1.1.1 Sedimentology of the Localities

Fluvial sedimentology is crucial for understanding paleofloras and stratigraphy, as fluvial deposits can provide evidence for reconstructing the environment at the time of deposition. Conversely, the paleofloras provide information about the environment for understanding depositional environments. The sediments of the Frenchman and Ravenscrag in the Willow Bunch Lake map area are considered to be fluvial deposits (Broughton 1978). Coal swamps and low-velocity floodplains have been interpreted as the primary depositional environments. However, for the purposes of this project, it was best not to assume this, but instead to determine the facies independently. Measured sections and observations of the area were compared to other known facies for this purpose.

Five sections in the Big Muddy Valley (fig. 4) were measured with the goal of understanding the sedimentology of the area (for detailed descriptions of these sections, see Appendix C). They have been designated, from east to west, 6A (US 838) (fig. 5), 2A (US 822) (fig. 6), 1C (US 819) (fig. 7), 2D (US 825) (fig. 8), and 1E (US 821) (fig. 9). These were compared to a sixth section taken by Dr. A.R. Sweet from the Geological Survey of Canada (GSC) in the Big Muddy Valley, designated the Big Muddy Valley section (5-27-3-24 W2) in the GSC records, which he analyzed for palynomorphs by him. According to the palynological study, the GSC section contains parts of the Whitemud Formation and Frenchman Formation, and part of the grey facies of the Ravenscrag Formation. These deposits cover the time range from Maastrichtian through to early Paleocene time, although the other sections used in this study have not had biostratigraphic or magnetostratigraphic techniques applied to them, they cover the same package of rocks.

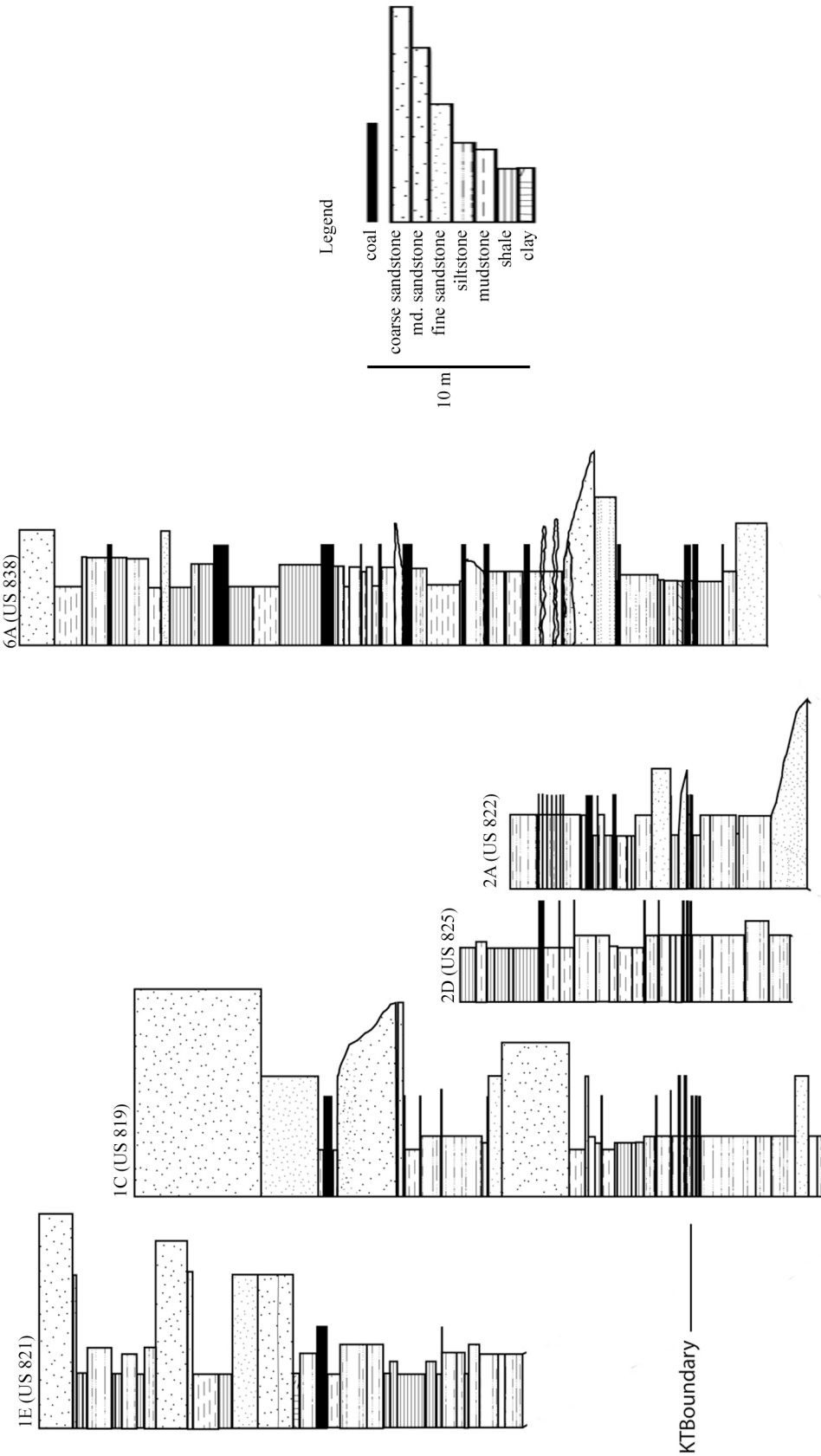


Figure 4. Sections taken in this study. All sections found in the Big Muddy Valley near Highway 34.

6A

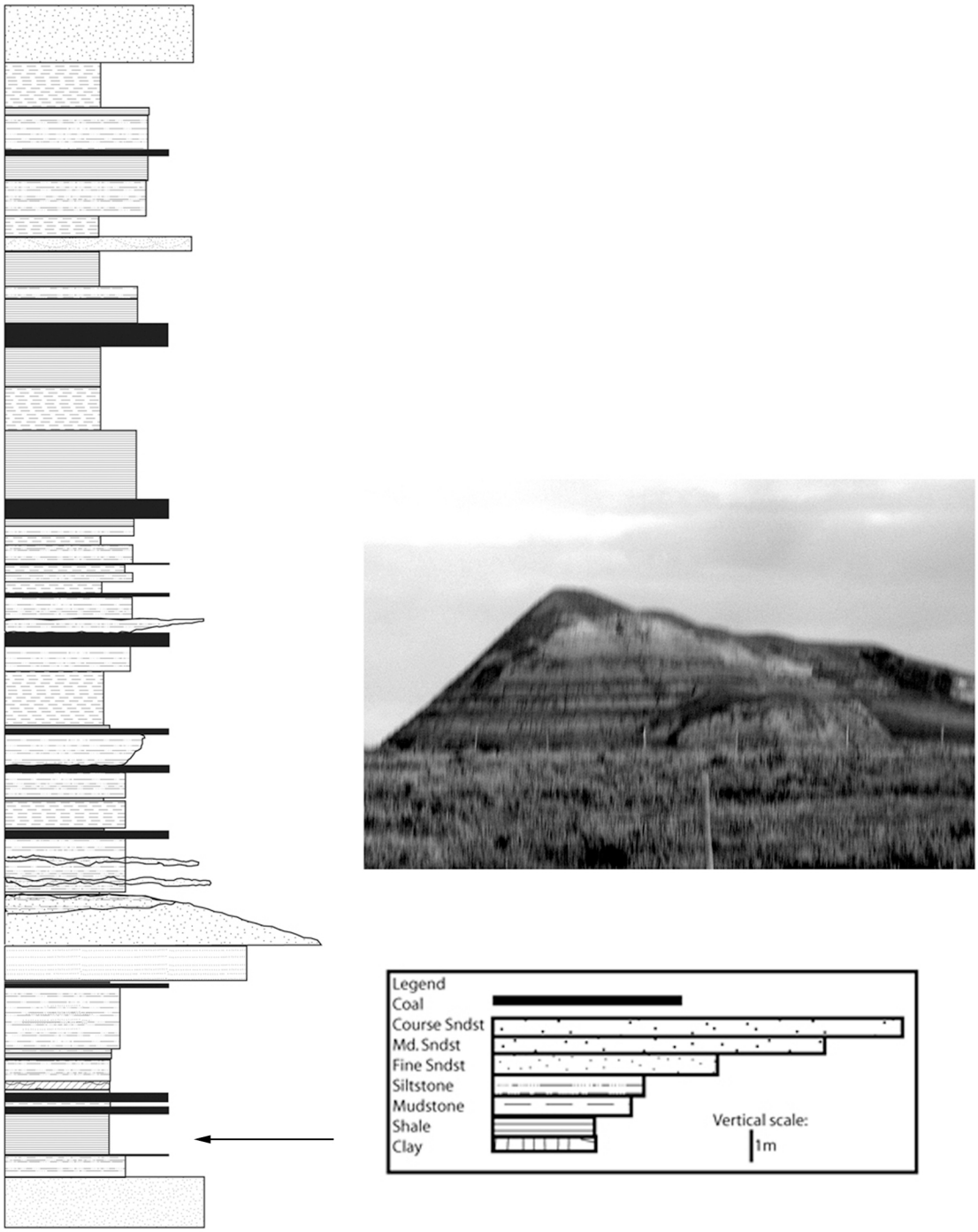


Figure 5. Section 6A. Section was taken at loc. US838. K-T boundary marked by the arrow.

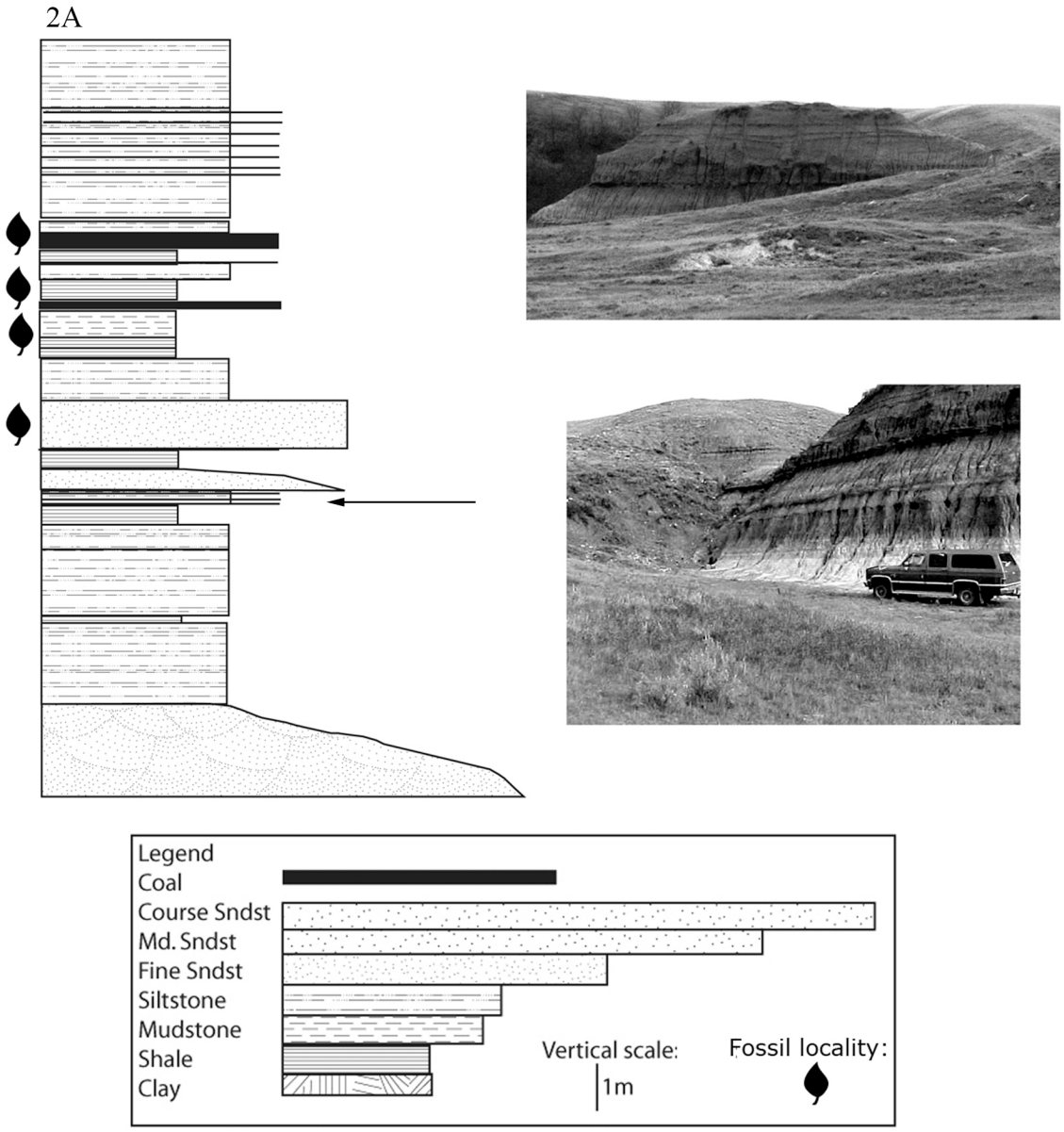


Figure 6. Section 2A. Section was taken at loc. US 222. K-T boundary marked by the arrow.

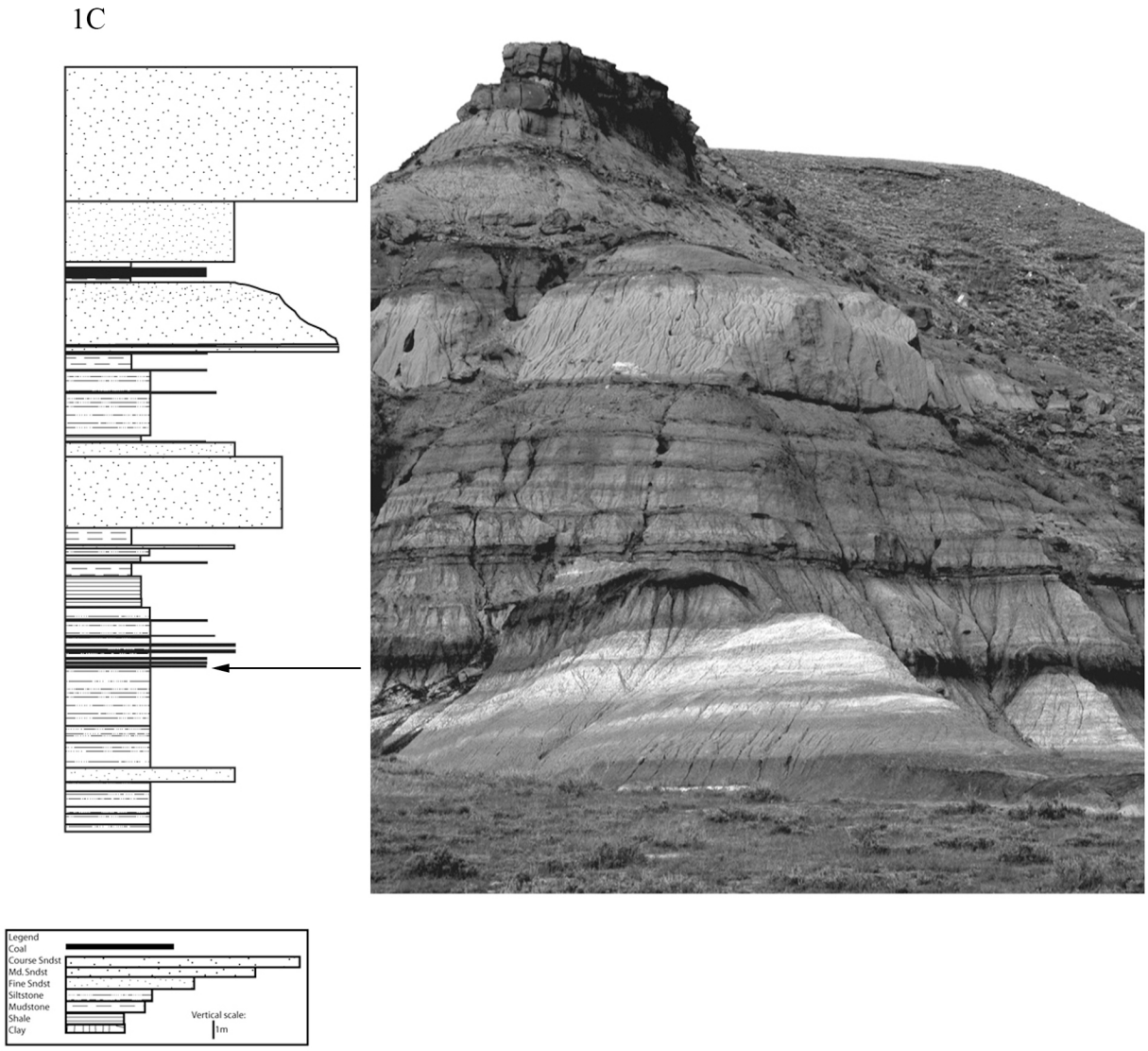


Figure 7. Section 1C. Section was taken at loc. US819. K-T boundary marked by the arrow.

2D

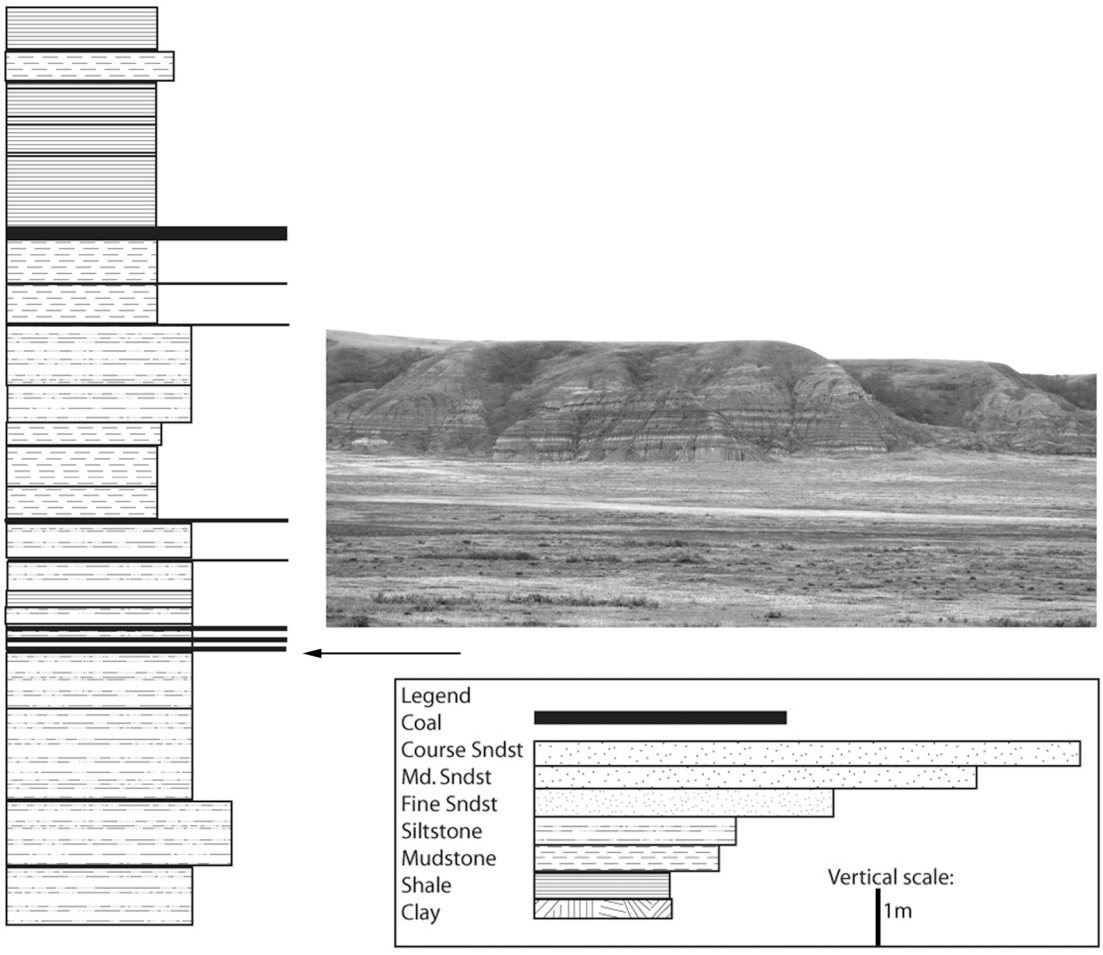


Figure 8. Section 2D. Section was taken at loc. US825. K-T boundary marked by the arrow.

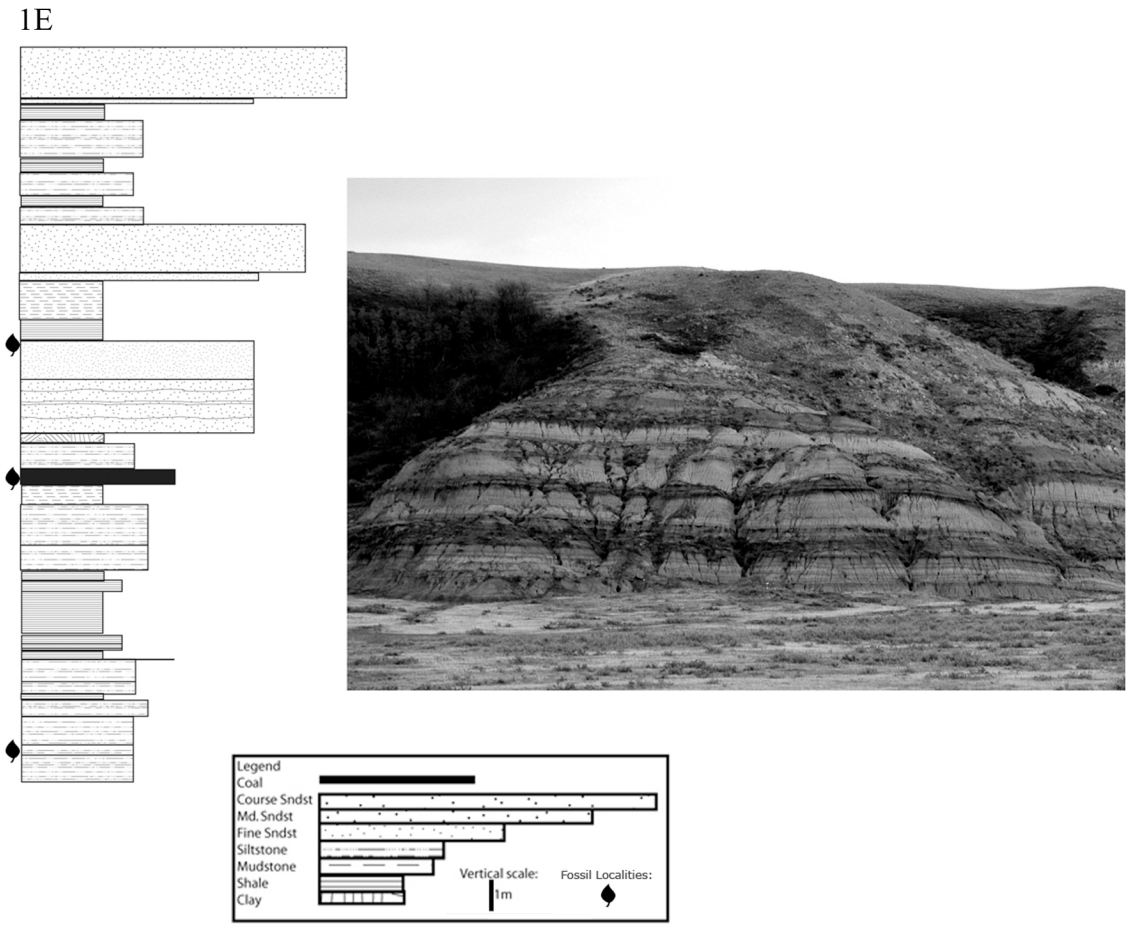


Figure 9. Section1E. Section was taken at loc. US821. K-T boundary below section.

The sediments of the localities used in this study primarily consist of a variety of fine-grained sediments, mixed siltstones and claystones. Coals are common, with thin coals (less than 5 cm thick) occurring through much of the section. The combination of these small coal layers and claystones results in an abundance of carbonaceous "paper" shales. Parts of the clay and silt are unconsolidated, in layers best described as "mud". Ironstone is present, both as extensive resistant layers, which can range up to 10 cm thick, as well as thin, non-horizontal concretions and iron staining. Sand bodies occur throughout the section, and commonly top the hills as capping beds, as they provide resistance to erosion. Erosion has sculpted some of these sand beds into hoodoos. Castle Butte, a prominent feature within the Big Muddy Valley, is largely sandy. Most of these sand bodies are made of fine grained sand or sandstone, although some are coarse grained. There is no gravel grade sediment in the region. Small-scale fine cross bedding and climbing ripple laminae are present in some of the deposits (fig. 10), but these are rare and it is much more common for these beds to appear structureless. Additionally, some of the beds, primarily some of the carbonaceous shales, contain gypsum rosettes.

Fine-grained sediments of the type present in the study area only form in low-energy environments. Typically, these sediments form in meandering stream floodplains, deltas or lacustrine environments (Miall 1996). The alternation of coal and ironstone beds shows that the sediments in the area had fluctuations in their oxygen and water content, as ironstones form under oxidizing environments, whereas coals form mainly under anoxic conditions. The overall fine-grained matrix of these rocks was likely due in part to the large amounts of plant materials present in the environments. This plant material would have slowed the energy of the fluvial system.

Besides the fine grained sediments, there are also distinct channel scours and the sand bodies with structures. Some sandstones also contain rolled leaves. This facies is interpreted as remains of faster flowing channels that snaked across the landscape, carrying relatively coarse sediment and causing large leaves to be curled in the underflow, rather than settling in leaf litter mats.

One of the main reasons for the fine-grained nature of this sediment is its distance from the sediment source. The sediment in the study area originated to the

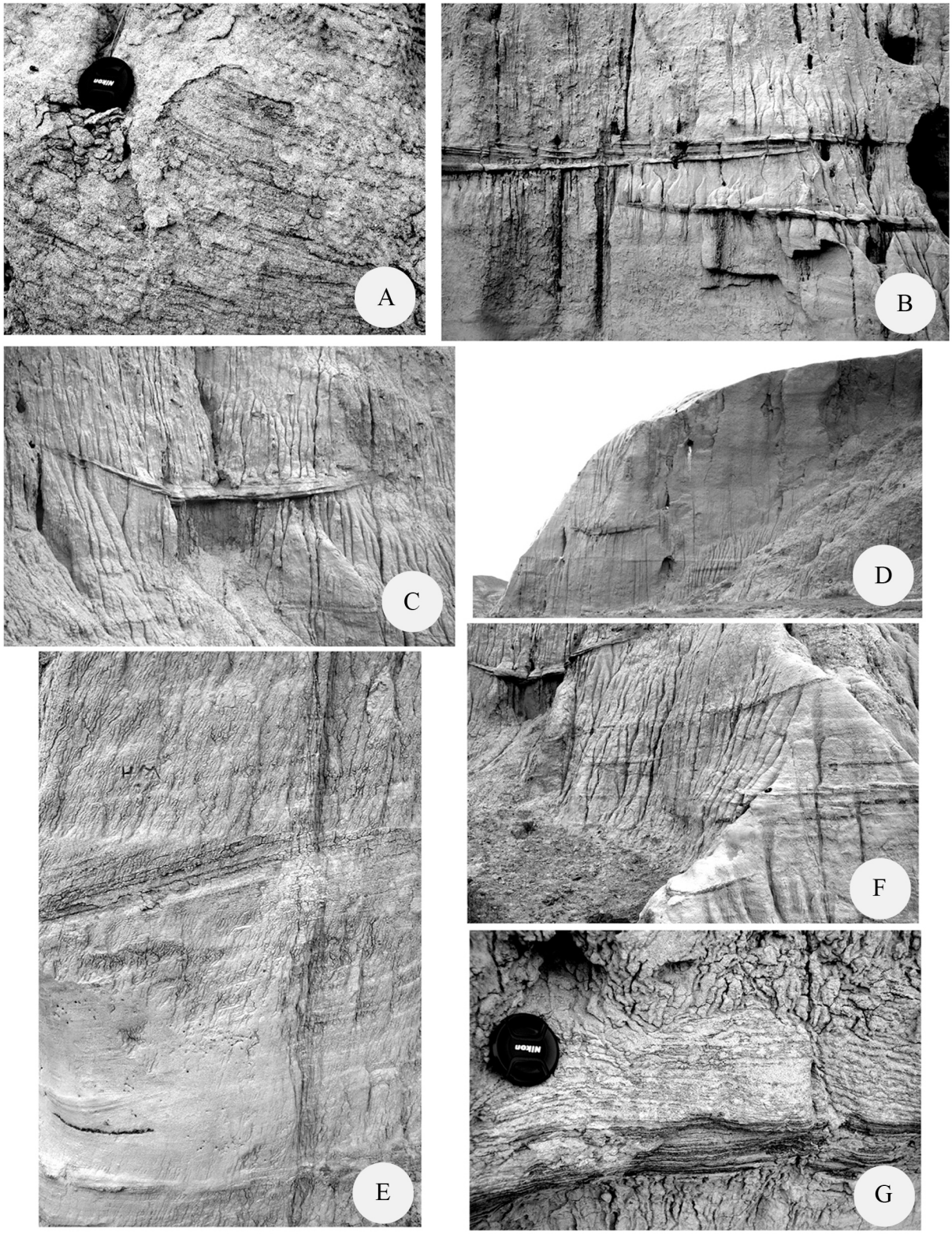


Figure 10. Structures on Castle Butte. A: cross laminations in sandstone.B, C: channel infills. Extrudent channel base beds about 4 cm thick. D: portion of Castle Butte showing channel in otherwise flat beds. Portion of the butte illustrated is about 6 m thick. E: climbing ripples, each bed about 1 cm thick. F: channel infills, resistant beds and ripples, resistant beds about 3 cm thick. G: rippled beds in sandstone.

northwest in Alberta (Dawson et al. 1994). Over the long distance travelled, the rivers lost most of their velocity as they flowed through thick swamp forests, which covered the entire route from Alberta to the Cannonball seaway (Dawson et al. 1994). The study sites occur at the distal end of this fluvial system, so much of the coarse grained bedload had already settled, and the rivers had lost much of their velocity.

6.1.1.2 Climatic and Foliar Influence on Sedimentation

Climate, particularly water supply, has a major influence on the sedimentation in a region (Schumm 1977). First, water will dissolve many minerals, breaking down rocks in the landscape. Second, water will transport grains according to the amount of discharge, and larger grains will settle when fluid velocity declines. Third, a lack or abundance of water will cause variations to the consistency of the sediments, causing for example, bank slumping and the formation of desiccation cracks (Mack and James 1994). Temperature has a slight effect on fluvial sedimentation, although it contributes to chemical weathering rates and drying and subfreezing temperatures can cause additional weathering through freeze-thaw.

Climate has an overall effect on the wind systems and precipitation amounts in a region. Wind typically has little effect on the sedimentation (Schumm 1977). Eolian sediments are rarely preserved in the rock record. Wind patterns also contribute to precipitation patterns, which can modify sediments. However, it is the way climate interacts with the water table that is often the most significant (Schumm 1977).

Besides the important impact of water on sedimentation, one of the greatest controls on sedimentation in individual beds is vegetation (Rees et al. 1999). An oft underappreciated influence, plants play a significant role in the stabilizing, destabilizing, weathering and buffering of fluvial sediments, as well as influencing channel stability. Additionally, plants can contribute detritus mass to sediments themselves.

The interaction between plants and climate can be crucial. In particular, temperature and humidity are integral to plant growth, with biomes commonly linked to specific climatic ranges. Shifts in climatic conditions can be disastrous for a floral community. Every floral community has a tolerance range, with some communities being climate sensitive and others having more resistance to change.

Additionally, plants can work with other processes in a feedback loop, where the types and density of vegetation affects climate zones. These effects are rarely considered in reconstructions, as the purely physical aspects are less well known, but there have been some exceptions. The study of coals often considers these interactions, but other interactions are more subtle, such as the mechanical and chemical effect of roots on the substrates.

Plant materials and associated microbiota can cause diagenetic changes to the sediments, by disrupting them, creating space for pore fluid penetration, and changing the chemical nature of the soil immediately adjacent to the plant materials. Diagenetic changes can also occur from the breakdown of detrial plant matter, as this releases acidic compounds that commonly leaching into the underlying strata. This can be seen in bleaching or other colour change of sediments surrounding coals. Additionally, derivatives of the acidic compounds in nearby soils result in gypsum and other sulphur compound deposition. In the sediments of the present study, these compounds were found, with many of the carbonaceous shales containing both gypsum rosettes and powdered native sulphur. These were likely produced by oxidation of sulphides such as pyrite in the shales and coals.

The palaeoenvironment of the Big Muddy Valley is interpreted as a largely inundated conifer swamp on a floodplain. Seeking an extant model, the most similar general ecosystem may be the extant modern *Taxodium* swamps of the southeastern United States. Unfortunately, no wild *Glyptostrobus* swamps are in existence (Farjon 2005), therefore the closely related *Taxodium* swamps seem the best proxy available. This means that a fully accurate understanding of the chemical changes associated with the plant material cannot be provided, as the products of the degradation of the biological matter will be slightly different, because each plant produces different compounds. However, some general observations can be drawn from the analogy, as has been done in other studies (Frank and Bend 2004).

The model conifer swamps are typified by acidic ground waters (Day 1982) as conifer needles commonly lead to the formation of numerous acidic compounds. These acidic ground waters can induce the formation of clays through chemical weathering of the siliciclastic grains. Combined with the sluggish movement within these bodies of

water, this facilitates deposition of these new clays. This is reflected in the Big Muddy Valley sediments, where clays form a sizable percentage of the sediment. The process of clay formation and transformation from one type of clay to another often results in a countering of the acidity present in the system, as the breakdown of the silicates neutralizes the system; however, it can also lead to additional leaching of nutrients from the environment, as clay minerals commonly incorporate cations into their crystal structure. Although not particularly well understood, this interplay is crucial to understanding this environment. Clays can also partially seal an area, reducing leaching, which in turn promotes coal formation in the anoxic peats (Day 1982).

The effects of climate and vegetation on sediments can be primarily observed at the level of the individual beds, with broadscale facies analysis dealing with other depositional factors (Schumm 1977). Vegetation plays a limited role in the understanding of larger, cyclic interpretations of the sediment column.

6.1.1.3 Sedimentological Interpretation

Taken as a whole, the sediments are interpreted to have been deposited in a meandering river system running through a forested landscape. The area seems to have been rather wet and warm, as there was abundant plant growth, with the formation of numerous coal layers. Coal formation is exclusive to areas with abundant moisture and warm temperatures (Miall 1996). This is the classic interpretation based on the palaeoflora, and is well supported by the presence of crocodilians in these beds (McIver and Basinger 1993; Markwick 1994). The coals, carbonaceous shales, muds, siltstones, and the thin sandstones, particular those lacking ripple marks, represent overbank materials deposited on the floodplain. The fine laminations support this interpretation, as do the localised root structures and stumps in the area. The variation in sediment types is likely due to a change in position of the streams during deposition, as distance from the source changes the composition of the deposits (Nanson 1980; Smith et al. 1989; Platt and Keller 1992; Smith and Perez-Arlucea 1994; Willis and Behrensmeyer 1994). The larger sand bodies likely were formed in the channels snaking across the landscape, as evidenced by the fine cross bedding found in these beds, the larger grain sizes, and the remnants of channels found in some of these areas (fig. 10 b,c,d,f). The

overall landscape was often disrupted, causing the periodic formation of ironstones. These were commonly thin, implying relatively short periods of disruption. However, they may represent longer periods of time as there are a few ironstone beds that are more extensive and up to 10 cm thick.

The absence of root structures suggests the environment was flooded and waterlogged continuously in most of the localities. Only in a few localities (US 830, US 834, US 832) are roots common. Some localities (US 832, US 840) preserve the roots of aquatic plants, but only in small numbers. The absence of roots likely comes from plant remains being transported within a wet environment, away from the sediments where the roots were firmly established. Continual flooding eliminates the ability for plants to establish roots in the soils, forming roots at the surface at most.

The rate of sediment accumulation varies according to many factors, a major one being the bedload carried by a fluvial system, which will determine the maximum amount of deposition in an area. In the fine grained sediments of the present study, it is important to also consider the number of times a year sedimentation events occurred, like floods. Additionally, factors such as vegetation can have complex effects by trapping loose sediment, eroding sediment banks, and affecting active bioturbation. A positive net sedimentation rate occurs when the factors preserving the input of sediment in an area exceed those removing sediment from the area.

There are a number of methods of determining the sedimentation rate for a region. One method is to develop models based on the sedimentation rates of modern facies. However, this is often a poor estimate, as the number of variables that can affect the rate of sedimentation is abundant, and may be impossible to determine from the rock record. Instead, the traditional method for determining sedimentation rates is to measure sections with well-dated marker beds and establish the average rate based on the amount of section divided by the time represented. This calculates a rough estimate, especially in repetitive facies with few hiatuses, of the sediment rate. The most robust method is to use the marker bed estimation method together with facies analysis to maximize the accuracy of each model.

In the Williston Basin depositional rates have been determined for many localities. Through much of the region, the sedimentation rate for the fine-grained facies

seems to have been about 85m/Ma (Hicks et al. 2002). However, it has been proposed that the Ravenscrag Formation materials had a different rate of sedimentation to the other Williston Basin localities (Catuneanu and Sweet 1999). This is difficult to determine as there are few robust marker horizons in the region; however, a slightly higher rate of sedimentation than the average for the Williston Basin has commonly been inferred for this specific area.

6.1.2 Environmental Interpretations

6.1.2.1 "Taxodiaceous" Back-swamp

The most common environment represented in the Big Muddy Valley is best interpreted as a conifer dominated back-swamp. There are a number of subtypes to this assemblage type, distinguishable by the ratio of *Metasequoia* to *Glyptostrobus*. US 817, US 819, US 820, US 821, US 822, US 826, US 829, US 838 are dominated by *Glyptostrobus* with little *Metasequoia*. US 828, US 830, US 843 feature a large quantity of *Metasequoia*, but also contain substantial quantities of *Glyptostrobus* as well. Other than a slight variation in conifer composition, these two subtypes are similar in composition and sedimentology. These beds typically contain few, if any, roots. Grain size typically ranges from sandy silt to shales. Small to large coals are common within these deposits. The shifting grain size of the environment, along with the often stirred remains, implies a depositional environment near a fluvial deposit. Filled channels are often found in the region. Of them, the *Metasequoia* areas are interpreted as slightly more mesic, although it is a continuum, as evidenced by the large roots in area US 830.

6.1.2.2 *Paranymphaea*, *Quereuxia, Azolla* Beds

One bed, US 845, represents a slight variation from the "Taxodiaceous" swamps. This bed contains no conifers, instead being composed of *Paranymphaea*, *Quereuxia* and *Azolla*. *Paranymphaea* and *Quereuxia* both occur as rare members of the back-swamps, but are much more abundant in this bed. The presence of these plants in the back-swamp floras shows that these plants grew in close proximity to the Taxodiaceous back-swamps. Due to *Quereuxia* and *Azolla* both being aquatic plants, it is likely that

this bed represents deeper standing water than the typical swamp, and it is likely that the conifers were unable to take root due to the higher water levels.

6.1.2.3 *Nelumbago* Beds

As mentioned in the remarks of *Nelumbago montanum*, this aquatic plant forms one virtually monotypic bed in the study area. Only a few isolated leaves of other plants occur in this bed, such as a *Trochodendroides* type leaves, and some leaves that are difficult to interpret, but possibly *Paranymphaea crassifolia* (pl. 10 fig. 2). Sediments in this bed are fine, prone to flaking off in thin sheets, especially when dry. It is interpreted that this bed records a deeper water situation than the "Taxodiaceous" back-swamp. This bed occurs between beds representing the back-swamp environment. Based on the leaves, which are typical for aquatic plants, it seems that this bed was formed through the presence of deeper water conditions in the swamp environment.

6.1.2.4 *Lygodium, Nyssidium* Rootlet Beds

Locality US 834, and possibly US 841, represent a slightly different environment from the rest of the "Taxodiaceous" back-swamps. The conifers are common, but less important members of this deposit. Instead, the cercidiphylloids, platanoids and terrestrial ferns are plentiful. Due to the higher presence of roots and otherwise absent ferns, this locality is interpreted as being dryer than the swamps. However, this is interpreted as less of an environmental difference than between the conifer swamps and the *Nelumbago* beds, as other than a slight variation in ferns, the dominant members are identical to the swamp flora, just in slightly different ratios. These beds exhibit a higher proportion of angiosperm remains compared to the other swamp localities. These localities could easily be interpreted as part of the "Taxodiaceous" back-swamp environment, in a similar fashion to how locality US 830 was handled in the earlier section of this accounting. Whether these beds are considered to be a distinct sub-flora or not, the variations between the typical conifer-dominance and the diversity of these beds are noteworthy.

6.1.2.5 *Mesocyparis* Clay Deposits

Locality US 840 represents a different sub-flora from the back-swamp sub-floras described above. It contains rare members of the swamp sub-flora. It is conifer dominated, but the primary conifer is *Mesocyparis borealis*. *Glyptostrobus* still occurs, but in smaller quantities, *Metasequoia* is virtually absent, and the angiosperm members differ from other localities. The most common angiosperm element is a fagaceous leaf that is extremely rare otherwise, with 2 poorly preserved specimens all that has been recovered in hundreds of specimens from the back-swamp floras. This locality is interpreted as an environment occuring near the swamp floras but featuring both drier regions and deeper water. The fine grained sediments and *Azolla* imply a deeper water environment than many of the other beds. However, the other sub-flora constituents are considered drier environment elements. Other than a few *Azolla* roots, there are no roots preserved in this bed, which is generally consistent with constant inundation of the environment. The nearby coals seem to be similar in composition to normal sub-flora 1. The palynology and macro-flora show the coals are formed from *Glyptostrobus*/*Alnus* swamps (Potter et al. 1991; McIver and Basinger 1993).

6.1.2.6 Junglandaceae and Rush

This sub-flora is distinct from the others, with few of the species overlapping. *Mesocyparis borealis* and *Dennstaedtia americana* are rare elements of this sub-flora, and the only elements that occur in other sub-floras. This sub-flora is dominated instead by two angiosperms: a rush-like monocot (pl. 9 figs. 1-3) and a narrow lanceolate leaved dicot (pl. 14 figs. 1-4). The environment was likely an open lake environment based on the fine sediments and the presence of rushes. Numerous vertical root casts, filled with sand, puncture these leaves, implying relatively rapid burial and shallow water. Microcoals occur in this bed as well, likely representing times of slightly greater organic accumulation in the lake body. Additionally, there are many thin ironstones in this bed, all under 5 mm in thickness and many under 1 mm. There is a general correlation between the iron materials and the organic materials. Many of the root casts have ironstone leaching around the edges. Leaves are often preserved with iron staining and replacement at times. Due to the distribution of the ironstones, it seems likely that they

occurred as post deposition pore fluids, which accumulated in the sandy tunnels or other disturbances in the clay.

6.1.3 Locality Interpretations

The localities studied in this project can be categorized into three general types, based on the floras contained within. As discussed in the geologic interpretation, the sediments present in the area are similar throughout the area, leading to floral elements to be the major indicator of sub-system environmental interpretation. The differences between floral composition in the fossil localities are not sufficient to signify distinct floras, but, rather, all of the plant diversity is thought to represent a single regional flora. Variations in water levels and, thus, depositional environments affected vegetation distribution and biased taphonomic processes leading to disparity in floral preservation Sub-units of this flora are termed sub-floras in this study. There are three sub-floras recognized as part of the entire paleoflora of the Big Muddy Valley. These sub-floras are distinct from one another, and likely represent different depositional environments.

6.1.3.1 Sub-flora 1

Sub-flora 1 is the most extensive sub-flora present in the area. It is present in all of the earliest Early Paleocene localities found in the area, US 817, US 818, US 819, US 820, US 821, US 822, US 823, US 825, US 828, US 829, US 830, US 845, US 833, US 834, US 835, US 836, US 838, US 839, US 843, and possibly US 824, US 831, US 841, US 842.

The most common elements of this sub-flora are *Glyptostrobus dakotensis* and *Metasequoia occidentalis*, with regular occurrence of broadleaved angiosperms, primarily *Archeampelos acerifolia*, *Zyziphoides flabella*, *Cercidiphyllum genetrix* and *Ettingshausenia raynoldsii* (fig. 11). The nearest living relatives of all of these plants are

lowland to swamp plants, so it is common to interpret this vegetation mix as representing a lowland to swamp environment (fig. 12). This combination of floral elements is common throughout the Late Cretaceous and Tertiary of the Northern Hemisphere. Variations within this sub-flora are primarily in the ratios between the three

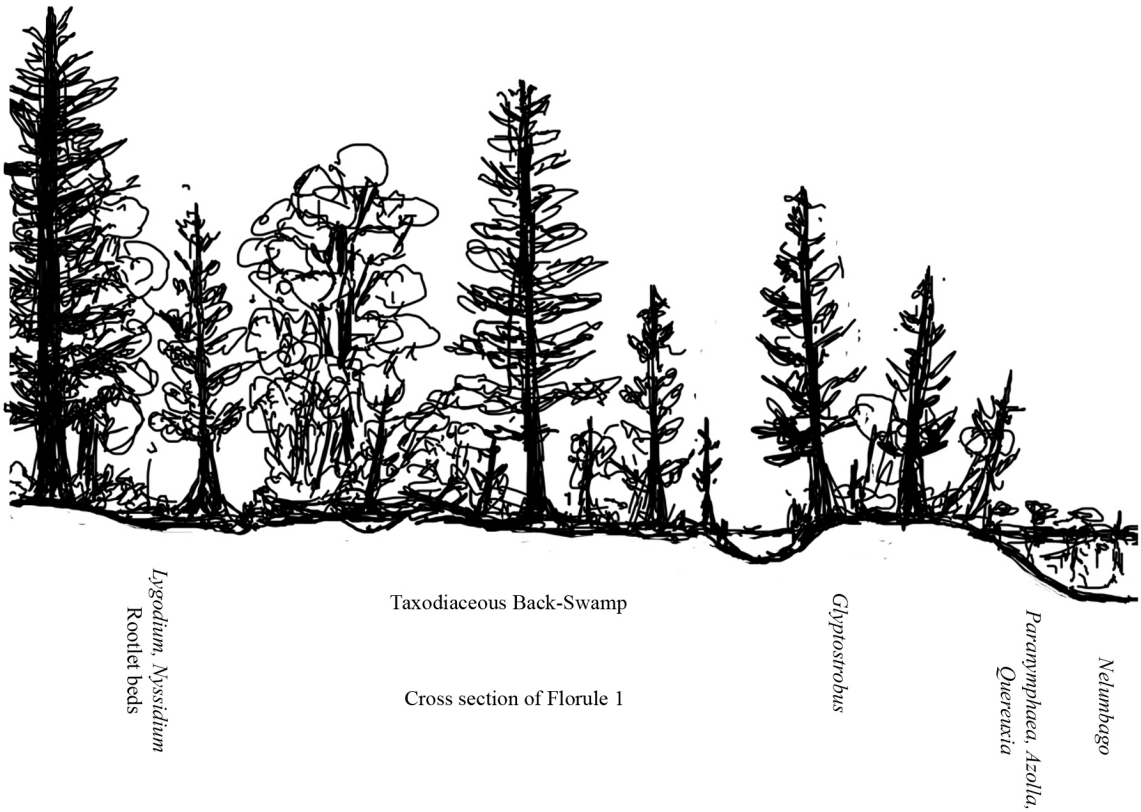


Figure 11. Cross section of environmental distribution of sub-flora 1.

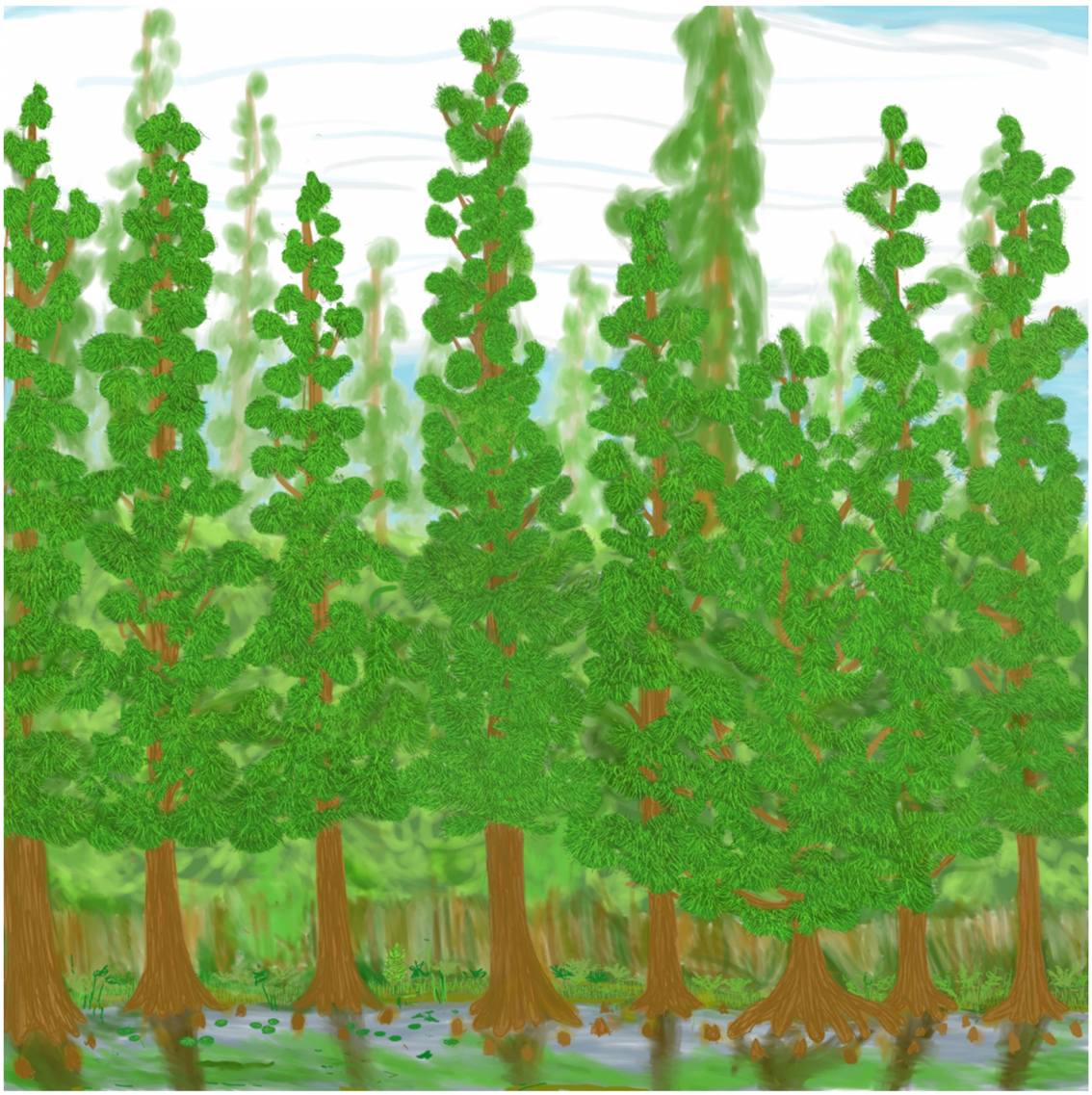


Figure 12. Reconstruction of sub-flora 1

most common elements (fig. 13). As can be seen, the majority of the localities express a heavy *Glyptostrobus* bias.

There are sub-elements of this sub-flora. *Nelumbago montanum* occurs in one nearly monotypic bed. It is possible that this should be a separate sub-flora as well, likely representing a deeper or less energetic water environment. However, the continual association between the swamp elements and these beds leads to the interpretation that they are part of this sub-flora. Additionally, extant *Nelumbo nucifera* grows in swampy areas, in wetter areas than the trees (Thomas 2003).

The *Paranymphaea-Azolla-Quereuxia* beds present in locality US 845 also are distinct from other parts of sub-flora 1. These beds are included with sub-flora 1 for two reasons. First, both *Quereuxia* and *Azolla* appear as rarer elements of many of the other local beds that contain sub-flora 1, such as localities US 817 and US 822. Second, this mix of plants is found together elsewhere (McIver and Basinger 1993). Sub-flora 1 is understood as the beds found in other regional localities, such as the flora found at Ravenscrag Butte. Therefore, these beds and plants are included in sub-flora 1.

The beds that produce roots are also questionably of sub-flora 1. However, all of the elements of these beds appear in the other beds of sub-flora 1 in this study, and commonly appear as parts of other regional floras as well (McIver and Basinger 1993; Hoffman 2002).

Localities US 817 and US 822 are the best models for this sub-flora, as they both contain a wide diversity of plants and fossiliferous beds. US 817 and US 822 feature similar compositions, producing *Glyptostrobus*-heavy collections. The fossils were in a soft matrix that proved easy to process. Both localities produced over 30 species, of which only the rarest elements were lacking from the other. It is expected that the missing elements would likely be found in the other locality with more collecting.

6.1.3.2 Sub-flora 2

A second sub-flora occurs higher in section, and differs from the swamp locality. It is found only at locality US 840. It is found in a white claystone. It consists of about 7 species, the majority of which are found in sub-flora 1. However, the most common element of this sub-flora is *Mesocyparis borealis*, which is a rare element of the swamp

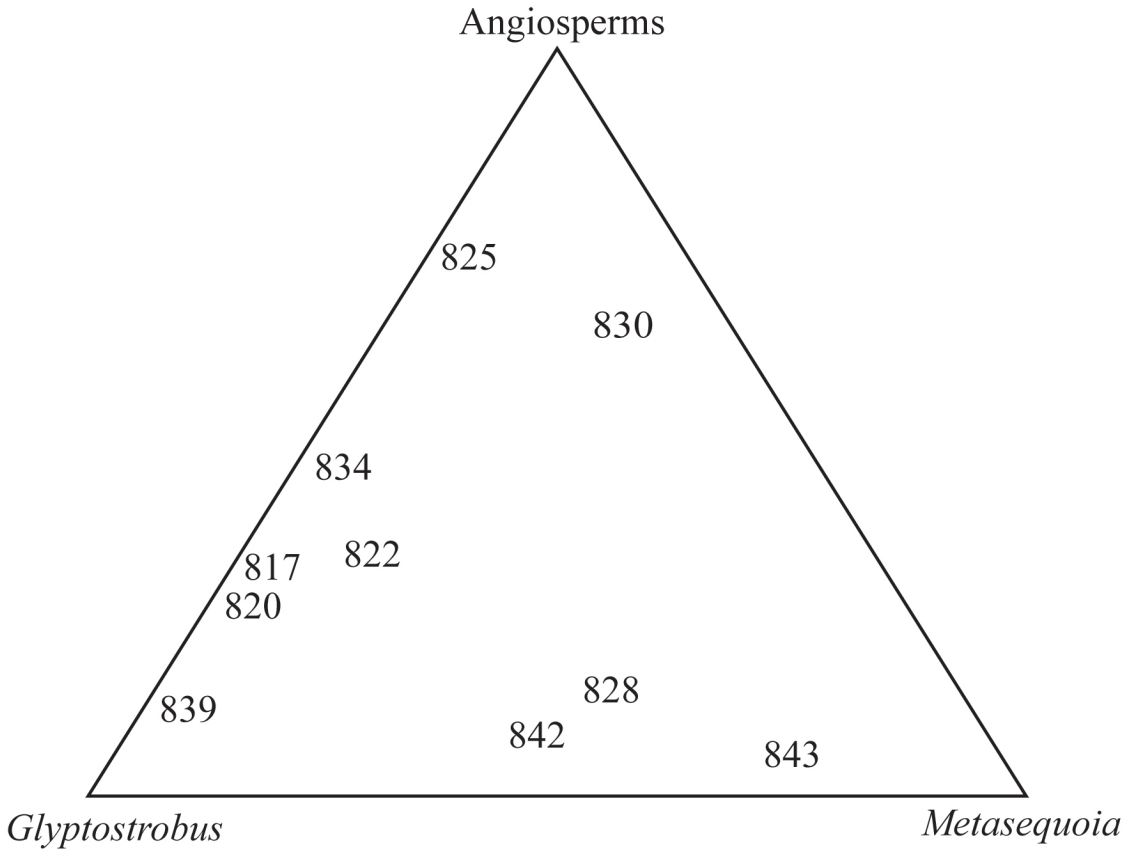


Figure 13. Ratio of floral composition in sub-flora 1. Numbers are USPC localities.

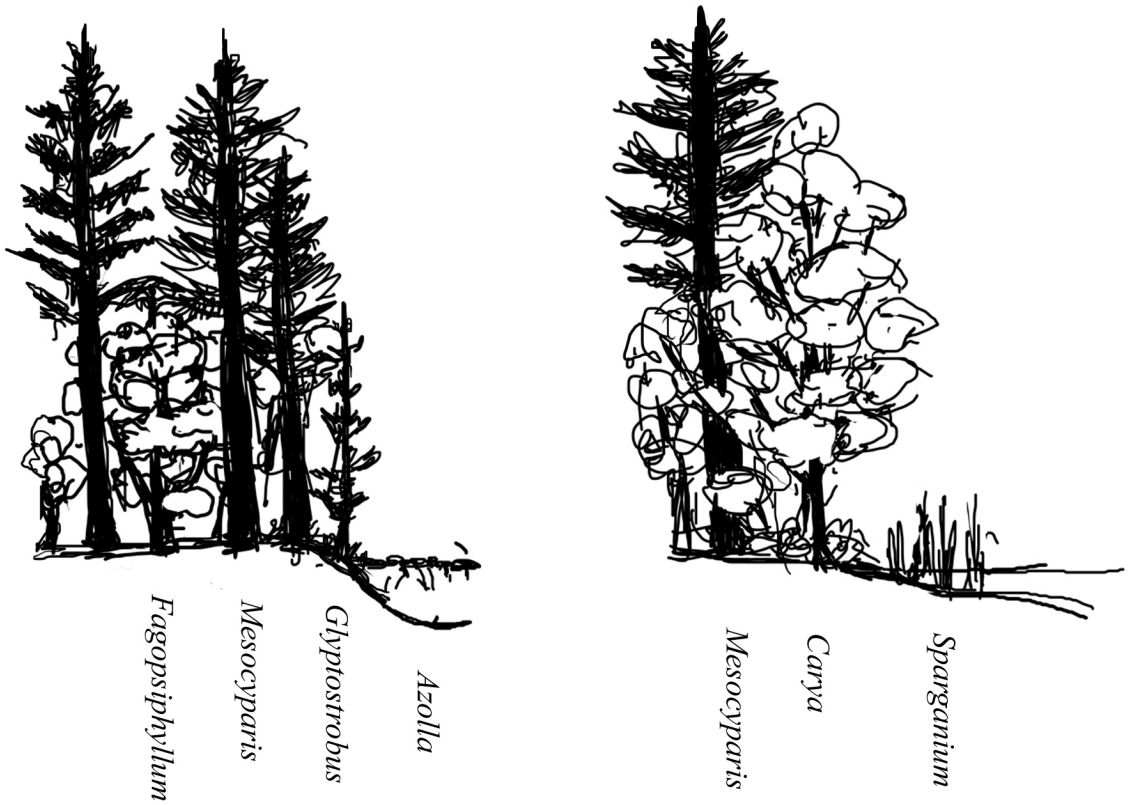
sub-flora. *Glyptostrobus dakotensis*, *Corvirupestrobus adrielensis*, *Fagopsiphyllum praegroenlandicum* and *Azolla schopfii* are also common elements of this sub-flora. Of these elements, only *Glyptostrobus dakotensis* is common in the swamp sub-flora, but it is much less common in this sub-flora. *Metasequoia occidentalis*, *Browniea serrulata* and *Nyssidium arcticum* occur as rare elements. All of the elements except *Azolla schopfii* and possibly *Corvirupestrobus adrielensis* occur in sub-flora 1, but in reversed abundances. It is thought that this environment consisted of a mesic conifer forest by a lake, thereby preserving *Azolla* as well as the *Mesocyparis*, *Fagopsiphyllum* and *Browneia* (fig. 14).

Transported remains from sub-flora 2 are rarely found in the swamps, and vice versa. This trading is expected. It is interesting to see the origin of many of the rare specimens in the swamp sub-flora. It provides a glimpse into distribution, as well as confirms that the common elements of this sub-flora are limited in expression in the typical swamp sub-flora due to environmental exclusion, instead of low appearance in the entire flora. The form of the rare elements can also be explored with greater validity due to increased abundances of specimens.

Mesocyparis sp. is often found in near monotypic beds in other localities, including one such bed in Ravenscrag Butte, and others in the Amur region (L. Goloneva, personal communication 2006). However, the Ravenscrag Butte material is a thin bed, whereas here the material occurs in a bed over 1m thick. Locality US 817 has a thin layer purely of *Mesocyparis* remains, which also is white clay with some iron staining. These other beds likely preserve the same ecological niche as this thick bed, but due to their reduced size, which is likely an artifact of preservation, they do not contain the other elements preserved in the other localities. In at least the bed preserved at US 817, the fossils are poorly preserved, with no carbon remaining. It is also delicate, often disintegrating before removal from the outcrop.

6.1.3.3 Sub-flora 3

Sub-flora 3 is found only at locality US 832. Like sub-flora 2, it also occurs higher in section than sub-flora 1. There are about 6 species in this sub-flora. The most common species is *Carya antiquorum*. *Sparganium* sp, *Mesocyparis borealis* and



Cross section of sub-flora 2

Cross section of sub-flora 3

Figure 14. Cross section of environmental distribution of sub-flora 2 and sub-flora 3.

Dennstaedtia americana also occur, thought they are rare elements such as the rootstock of some plant (fig. 14). It is possible that these roots belong to the *Sparganium* sp, but this is not clear.

This sub-flora does not closely resemble the Canadian floras, but, rather, resembles floras of northern USA reported by Hickey (1977) which feature the two most common elements from sub-flora 3, "*Carya*" *antiqua* and *Sparganium parvuum*. Hickey's beds are interpreted as preserving a much warmer palaeoclimatic locality than the swamp sub-flora, occurring in the warmer Late Paleocene/Early Eocene (Wing et al. 2005) and farther to the south. It has been posited that the present study deals with an ecotone environment, on the border between the Arctic province flora to the north and the warmer environments to the south. This bed seems to represent a continuum within this interpretation.

6.1.3.4 Notable Localities

Some localities were more productive than the others, in diversity of specimens, ease of analysis, and quality of preservation, specifically US 817, US 822, US 831 and US 840. Locality US 817, also called "1A" or "Gopher Hole", was one of the most thoroughly collected localities in the area, with hundreds of specimens recovered. This locality consists of an approximately 20 m long exposure near the K-T boundary, and is a yellow silt bed about 1 m thick (fig. 15). At the base of the locality is an approximately 5 mm thick bed consisting entirely of *Mesocyparis borealis* impressions. No other bedforms occur in this unit, except some intermittent and non-distinct lamination. *Glyptostrobus dakotensis* is the most common plant found in this locality; foliage, seed cones, seed cone scales, and seeds were recovered. Relatively complete branches occur in these beds, with specimens up to 30 cm long recovered, preserving multiple branch orders. *Archeampelos acerifolia* leaves are common amongst the angiosperms, although not as common as *Glyptostrobus* foliage. Single leaves of many species were recovered by extensive collecting. This locality also best typifies the *Glyptostrobus* swamp flora expressed in sub-flora 1, as it has slightly better preservation and is easier to work with than many of the shales.

Figure 15. Quarry at locality US 817

Locality US 822, nicknamed “2A” or “Eagle’s Nest”, occurs on the north wall of the Valley near the highway. Many sub-localities are contained within this locality (fig. 6) as there is a productive zone of multiple meters in this section. The sub-units were not collected separately as they were initially considered a single unit in the collections of Mr. Larson. Preservation is consistent throughout much of the collection area, typically impressions and compressions. A thin bed dominated by *Nelumbago* is distinct from the rest, but other fossils were preserved in a grey siltstone. Thin sand and coal layers cross throughout. There is a lesser degree of coalification in this sub-flora than others. *Glyptostrobus* is a dominant component of this locality. However, it makes up a slightly lesser amount than locality US 817. *Zyziphoides* is the most common angiosperm element. However, there is an extensive and diverse collection of Angiosperms from these beds. Diversity is higher than most of the localities. Ferns are common elements of this flora as well. One of the more diverse cone and seed floras found in the region is present as part of the impression layers. Additionally, as mentioned above, the *Nelumbago* beds are part of this locality. A geologic section was measured for this locality.

Locality US 832 is located within the southern arm of Big Muddy Valley south of Big Muddy Lake. It is the only locality that contains sub-flora 3. As mentioned in the stratigraphy chapter, it is unclear where this locality fits in stratigraphically, although it is likely within the Buff Facies, which is now considered to be Middle Paleocene. Floral content has been considered under the discussion of sub-flora 3 above. This locality is a yellow claystone, with thin ironstones and coals.

Locality US 840 is located far from the other localities, in a series of limited valleys to the west, just north of the Poplar River Mine. It is the only locality that represents sub-flora 2. This locality occurs in a kaolinite rich layer. The primary outcrop is a limited butte (fig. 16), but the bed continues throughout the greater hill, with high production throughout (fig. 17). Floral composition is explained under the description of sub-flora 2. The collections, although heavy in *Mesocyparis*, are disproportionately low in *Mesocyparis* specimens, as these beds were collected with bias

Figure 16: Picture of type butte of US 840. The initial collections from this locality were collected here. Additional collections were taken from lateral extension of this bed (Fgure 17). This locality is found to the west of the Big Muddy Valley.

Figure 17. Picture of Mr. Larson walking bed US 840 away from the primary butte.

for the rare elements. If collected proportionally or in a census collection, this sub-flora would be well over 95% *Mesocyparis* remains.

6.1.4 Palaeoclimate Interpretation

Palaeoclimatic interpretations are one of the important goals of palaeobotanical studies. Numerous methodologies have been developed for this purpose, based on some form of proxy model. Each of these methodologies has limitations in both their underlying theory and applicability to all floras, and only a most superficial analysis can be performed for the present sub-floras. The two most commonly utilized methods are Coexistence Approach (Mosbrugger and Utescher 1997), which utilizes the Nearest Living Relatives of the plants of a flora, and looks to find a best fit climate for all of the elements, and physiognomic analysis, which is typified by the Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe and Spicer 1999; Spicer et. al 2004).

6.1.4.1 Nearest Living Relative (NLR) and Coexistance Approach (CA)

Based on the taxonomic understanding of this flora, the Coexistence Approach is potentially the more useful method for interpretation, as 28 of the 40 species of this study are not woody angiosperms, and therefore do not qualify for physiognomic study (Mosbrugger and Utescher 1997, Wolfe and Spicer 1999). In past studies, the climate has been determined for the nearest geographic floras using this method, whereas leaf physiognomy is missing from some of these nearby localities (McIver and Basinger 1993; Hoffman and Stockey 1999). Additionally, many of the sites of the Willow Bunch Lake map area are dominated by non-angiosperms. Leaf physiognomy will give a less precise understanding, as the physiognomy techniques are based on angiosperm floras. Third, many of the fossils are fragmentary, often lacking characters needed to perform a physiognomic study.

Paleocene floras are considered on the edge of validity in NLR studies (Mosbrugger 1999). Of the plants from the region, 12 are placed in modern genera. Familial affinity is understood for an additional 12 species. The number of taxa placed into extant taxa is reduced with every taxonomic revision. The majority of the 14 species that only have familial affinity traditionally would have been placed in extant

genera. Traditional taxonomies commonly placed specimens in the living genus that most similarly resembled the fossils, typically through a "picture matching" methodology. This led to many questionable placements and interpretations. Typically, the links between the living and fossil forms of all non-angiosperm-leaf fossils is considered stronger, as the remains are more diagnostic. This is the case in this study, where 9 of the 12 species placed in modern genera are non-angiosperms.

The climate parameters generated for the nearest living relatives of the plants of the Big Muddy Valley cover a wide range. This poor distinction stems from two sources: many of the plants placed in extant genera are recognized only from a monospecific "relict" species, which have poor climatic understandings; the connection between the NLR and all of the species in this study are tenuous, and therefore it is unclear which of the potential ranges for climate should be taken. The climatic tolerances for *Equisetum*, for example, range from frost tolerant temperate species to subtropical species that only survive in frost-free areas. It is unclear which of these species is closest to the fossil, and so it becomes less advantageous to use this technique. The climate data for the coexistence approach is unavailable for many of the taxa in this study. Therefore, a modified system is needed. United States Department of Agriculture (USDA) hardiness zones were available for more of the taxa, including the dominant elements of sub-flora 1 (Thomas 2003). Using these values, a hardiness zone of 8 seems the most reasonable (fig. 18). However, there is still some question to this result, due to the factors listed above.

6.1.4.2 Leaf Physiognomy and CLAMP

Leaf physiognomy is a popular method for establishing fossil flora climate parameters. Unfortunately there are problems with utilizing the physiognomic techniques with the fossils of the localities of the Big Muddy Valley. Leaf physiognomy relies exclusively on angiosperms (Wilf 1997). This can be problematic for this study as angiosperms are often secondary components of these floras. This technique also requires complete specimens to be utilized and the majority of fossils recovered are fragmentary. As well, the data must be censused, as compared to the voucher type data

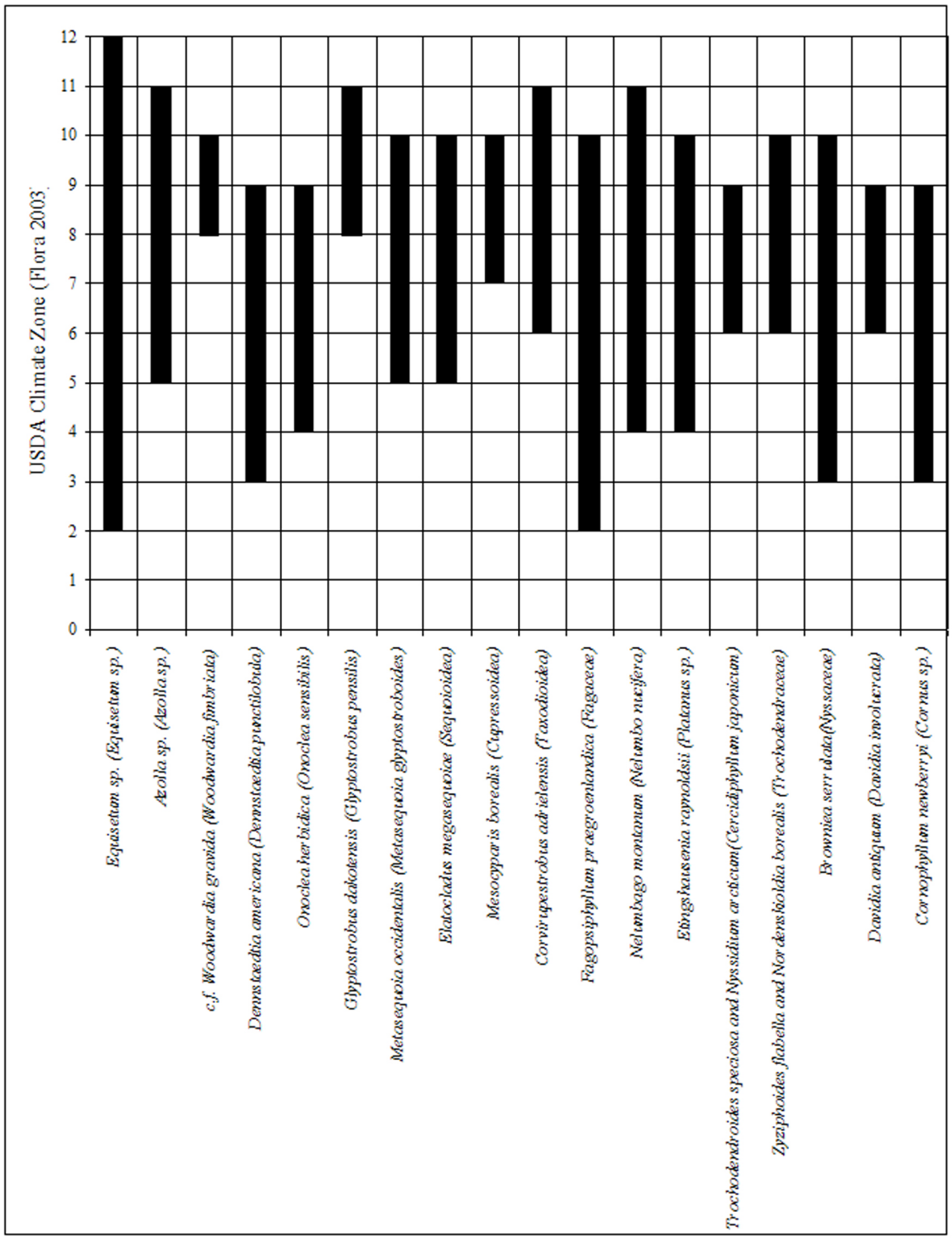


Figure 18. Chart of climate zone using a modified coexistence approach. Data from Thomas (2003), modified by the Paleoflora darabase (http://www.geologie.uni-bonn.de/Palaeoflora/Palaeoflora_home.htm)

set, which is used to find all the floral elements (Wolfe and Spicer 1999). A censused collection was unable to be collected.

For accuracy reasons, CLAMP and other physiognomic techniques require a minimum of 20 morphotypes to perform an analysis (Wolfe and Spicer 1999). There are a total of 11 appropriate species found across all of the localities in this study, with a maximum of 7 appearing in one locality. Additionally, two of the potential species are known from one incomplete specimen each. With additional collecting, it is possible that US 817, US 822, US 828 or US 830 may produce the requisite variation for a successful assay. However, given the large collections produced already, it is questionable how much the presence of anomalous remains should be considered in an analysis. The preservation is also often poor from the Big Muddy Valley, so collecting enough complete leaves may prove difficult. There is also a question of taxonomy. This study uses a more traditional and conservative estimate of plant diversity than the typical morphotype methodology utilized in physiognomic studies. A less conservative methodology would likely find a great increase in diversity. Despite the floral diversity in the Big Muddy Valley, the large percentage of conifers, pteridophytes and hydrophytes are not used for physiognomic study. For these reasons leaf physiognomy methods of paleoclimatic determination cannot be performed at this time on the localities of this project. To satisfy curiosity, a single variable of Leaf Margin Analysis (Wolfe 1979, Wilf 1997) was applied to the 11 woody angiosperm species and a mean annual temperature (MAT) of 10.87 +/- 4.6ºC was suggested, with an unacceptably high margin of error.

6.1.4.3 Local Climate Interpretation

Although a single analytical method cannot establish a confident paleotemperature for the Big Muddy Valley localities, the methods together provide a reasonable understanding of the climate, especially in conjunction with the more precise interpretations compiled for nearby localities. The generalized statement that the locality was “warm and wet” can easily be supported by the large presence of coal seams, relatively frost-sensitive conifer types and the presence of crocodiles and turtles, (Colbert et al. 1946; Markwick 1994). This is also the conclusion of workers of all

adjacent floras, using both NLR (McIver and Basinger 1993) and CLAMP (Johnson 1989), and global palaeoclimate for the Paleocene (Johnson 2002). Sub-flora 1 of this study is similar to other contemporaneous floras neighbouring this one. Coal swamps are interpreted as forming only in "warm and wet" climates.

Specific details of the climate are more difficult to ascertain. Climate interpretation for the Ravenscrag Butte site interprets it as a mild, humid (mesothermal) area with no dry season, with a MAT for the area was calculated as 16ºC, and parameters similar to southern China (McIver and Basinger 1993). Due to the large degree of floral similarity between the Ravenscrag Butte and the Big Muddy Valley, this result is appropriate for the Big Muddy Valley as well, and fits with the MAT of places in hardiness zone 8.

There is a major difference between the climate of south China today and the Ravenscrag Formation floras. Modern southern China is evergreen, or mixed evergreen and deciduous, whereas the Ravenscrag Formation floras were suspected to be mostly deciduous. This change is best accounted for through the differences of latitude. The localities of the present study were found above 55° north paleolatitude, perhaps over 60°, compared to the 25° to 35° north latitude of the extant Chinese localities (McIver and Basinger 1993). Despite the idea that the Early Paleocene is largely considered to be an ice free period of Earth's history (Graham 1999), polar forests would still have been subjected to a variable length of day, and although the monthly mean temperature is always above zero, it is suspected that the Ravenscrag floras reflect a much colder climate during the winter months than the subtropical models. Deciduousness would potentially allow more efficient energy use during the dark and cold months.

6.1.5 Animal Fossil Remains

Animal fossils are relatively rare in the fossil beds of this study. Animal remains do not preserve well in the acidic soils caused by the decomposition of plant remains (Eberle and Storer 1999). However some animal fossils were recovered during the course of this study. Additional animal fossils were also recovered from the area by other expeditions. Of particular note, scientists at the Royal Saskatchewan Museum recovered two crocodilians from the area, and they are stored in the archives of the RSM

(A. Larson, personal communication 2003). These relatively complete skeletons were found away from the plant beds.

Additional vertebrate remains were found in two localities. Scattered and relatively rare turtle remains were found near the base of US 839, with remains appearing along the coulee walls. These likely eroded from a thin bone layer, although its exact stratigraphic level was not mapped. A second bed, slightly thicker and more extensive was found below US 833, about 3m above the valley base. Gar scales and vertebrae, turtle shell fragments and bones including claws, and crocodillian teeth and scutes were recovered from this bed (pl. 22, fig. 4). This was a relatively rich bed and may be worth a detailed investigation. Taxonomy was not conducted, although at least two types of turtles were present. Only molluscs were found for invertebrate fossils. Gastropods appear in many localities. In particular, many appear in US 840 (pl. 22, fig. 5), although some were collected from US 817, US 822, US 835 and US 842. Bivalves were also collected from US 830 (pl. 18, fig. 2) and US 840. No animal trace fossils were identified in the course of this study.

6.2 Comparisons to Published Floras

Many Paleocene floras have been studied as complete units. To gain a broader understanding of context for the flora of this project, a select number of studies were chosen for comparison purposes. These studies are those that are currently the most important for comparison purposes, as most are regionally close, although some are considered due to the differences they express. The flora chosen for comparison is the most recent revision wherever possible for a given set of localities.

6.2.1 Ravenscrag Formation (Berry 1935)

This is the only published account of the Paleocene megaflora in the Willow Bunch Lake map area. Berry identified 80 species from the region, although many are only loose interpretations, and are not figured. Of his identifications, only *Paranymphaea crassifolia*, which was established in this study, and *Dennstaedtia americana* seem to still stand as a valid species. Leaves resembling most of the species in Berry's study have been recovered in the present study, including leaves that were not

found in the type section of Ravenscrag Butte and other Western Interior localities. However, most of these species and specimens are rarely considered in other studies. Partially, this seems to be due to the fact that it is unclear in which institution the specimens are ultimately residing. Additionally, these follow the oldest taxonomy, present in works like those of Newberry and Lesquereux. They have not been analyzed, although given the quality of remains recovered in the current study and other expeditions, it is likely that the specimens were of questionable quality for identification purposes.

It is interesting that *Glyptostrobus* was not emphasized in Berry's study, given its large percentage of the specimens observed in the current study. Cones are not recorded in Berry's study and he rarely reported *Glyptostrobus* cone materials in his floral surveys, so it is not clear if he had a working search image for them. This report was amongst the last prepared before Brown published on *Glyptostrobus* in North America (Brown 1936); therefore, Berry was likely unsure of the status of *Glyptostrobus* in his reports. Interestingly, Berry emphasized the presence of Angiosperms, which he found to be abundant and the most dominant members of this flora taxonomically and in specimen numbers. This is contrary to the findings of the current study, which find that the angiosperms are not numerically dominant, and have a lower taxonomic diversity comparatively, with only 25 species of angiosperm recognized compared to the 15 pteridophyte and conifer species of the current study. Berry had found nine species of ferns and conifers, of which he only reported six in detail, and 56 varieties of angiosperm. He admitted that some of the angiosperm diversity was likely exagerated, such as the diversity of "*Viburnum*" in the flora.

Overall, Berry interpreted the flora as being of a temperate type that dominated the forests to the north that seem to have an Arctic origin, with a few members, such as what he recognized as figs, being more typical of the floras found to the south. This is also the finding of the current study, which is largely more similar to the floras found to the north, but also includes elements of the warmer floras found to the south.

6.2.2 Ravenscrag Butte (McIver and Basinger 1993)

As mentioned in many of the remarks, the flora of the Big Muddy Valley largely resembles the flora collected from Ravenscrag Butte, Cypress Lake map area (72 F). A few other localities were also utilized in conjunction with Ravenscrag Butte, primarily within the same map area. 45 species were described in this flora. Taxonomically, the flora of Ravenscrag Butte is similar to the swamp sub-flora of the current study. It is unclear how the *Mesocyparis* dominated sub-flora 2 from the Big Muddy Valley area relates to the *Mesocyparis* dominated layers found in Ravenscrag Butte. Sub-flora 3 from the Big Muddy Valley area is not represented at Ravenscrag Butte, and the angiosperm components of this sub-flora is lacking. Conifer abundance is common to both of these localities, especially areas dominated by *Glyptostrobus* and *Mesocyparis*, which are rarer than *Metasequoia* dominated forests.

The Ravenscrag Butte localities are largely earliest Paleocene in age, with the top of the section (the buff facies) likely occurring in the Middle Paleocene (Catuneanu and Sweet 1999); however, it does not extend as far into the Paleocene as either US 840 or US 832.

Compostionally, Ravenscrag Butte and the Big Muddy Valley share the majority of their taxa, which is what was expected, given their close proximity. This is especially true of the plants of sub-flora 1. The common flora between the Big Muddy Valley and Ravenscrag Butte was part of the determination of the localities exhibiting sub-flora 1, as the similarity showed that these plants were part of a larger ecosystem. The plants that are absent in the Big Muddy Valley that were present at Ravenscrag Butte are largely the rare elements, typically species that only single specimens were found. Their absence is therefore not unexpected. Taxa lacking from Ravenscrag Butte that are present in the Big Muddy Valley are plants that are known only as rare elements to the south, and likely reflect the slight latitudinal difference between the localities at the time, or are elements of sub-flora 2 and sub-flora 3, which have no preservation at Ravenscrag Butte. Due to the overall high similarity between the floras of the Ravenscrag Butte and Big Muddy Valley, the climatic understandings that were ascertained at Ravenscrag Butte will hold for the Big Muddy Valley. Some of these climatic understandings are

spurious for reasons explained for the Big Muddy Valley data, but the interpretations are based on better fossils than those recovered from Big Muddy.

6.2.3 Smokey Tower (Christophel 1976)

This flora is considerably less diverse than the Ravenscrag Formation flora, with nine species in the tuff horizon and five species in the silt horizon. Taxa in common include *Equisetum*, *Cupressinocladus* (although the specimens are positively identified as *Mesocyparis borealis* in the Big Muddy Valley, and may represent a different species), *Glyptostrobus*, *Metasequoia*, *Ettingshausenia raynoldsii* and the trochodendroids. *Glyptostrobus* is the most common element in the Smokey Tower floras, which is similar to many other conifer forests throughout the Northern Hemisphere throughout the Paleocene and the rest of the Tertiary and is consistent with the Big Muddy Valley localities. Both *Glyptostrobus* and *Metasequoia* are commonly found together in Tertiary fossil forests. The ratio of *Glyptostrobus* to *Metasequoia* favours *Glyptostrobus* dominance in the Paleocene localities of the Western Interior, but differs from many of the arctic localities (Basinger 1991; McIver and Basinger 1999). The Big Muddy Valley largely has *Glyptostrobus* dominance, but there a few localities (US 843, US 828) with *Metasequoia* dominance. This is noted in the variations amongst the sub-flora 1 localities of the Big Muddy Valley.

The angiosperm content of the Ravenscrag and Smokey Tower are similar, although the number of angiosperms is limited for the Smokey Tower localities. This is a point of similarity between the Smokey Tower localities and most of the Big Muddy Valley localities.

It is notable that higher diversity is present in virtually all localities that are being compared to the Big Muddy Valley and the Big Muddy Valley itself compared to the Smokey Tower localities. The Smokey Tower localities are also notable for the large percentage of conifers, both in diversity and in abundance of the taxonomic diversity. These localities were extensively sampled, so it is not a sampling bias that causes this state. Instead, it likely reflects a different sub environment of the swamp sub-flora, one which is unique to Smokey Tower. That it was persistent across both horizons at Smokey Tower suggests relative stability. More than abundance of conifers, this

collection represents a paucity of angiosperms. The angiosperm taxa that are present are the ones most often found in the conifer swamps. One possible explanation for this difference is the presence of volcanics in the sediments of Smokey Tower localities. The weathering of these rocks would have caused different soil conditions, commonly with a higher acid content, similar to that caused by the decomposition of conifer remains. This would have pushed the conditions to favouring conifer depositions.

6.2.4 Joffre Roadcut Locality (Hoffman 2002)

Approximately 30 species have been identified from the Joffre Bridge Roadcut localities. This work was initially published in 1992, but the comparison utilized here is from the 2002 second report. However, these are the same document other than additional notes on subsequent studies found in the preamble. The Joffre Bridge Roadcut exposes a vertical section, which has about six plant producing layers (Hoffman and Stockey 1999). In common parlance, the whole area can be referred to as one locality, as they are closely related, but in precise terms, each of the specific collecting layers should be its own locality, as there are slight variations of deposited plants, which have been used to reconstruct subunits of the depositional landscape. Stratigraphic studies have shown that these beds are of a middle Paleocene age, compared to an Early Paleocene age represented by the Ravenscrag Butte and Smokey Tower Localities. These sites compare closely in age to sub-flora 2 of the present study, and are likely older than sub-flora 3.

There are many similarities among boreal Paleogene forests. The Joffre Bridge localities most closely resemble sub-flora 1 of the Big Muddy Valley, which is similar to other regional floras. This is interesting because, of all of the collected localities of the Big Muddy Valley area, the Joffre Bridge localities are most distant in time. Both are dominated by Cupressaceae, Platanoids and Cercidiphylloids. The Joffre Bridge localities have produced many fossils, with better preservation than those of the current study, and from a more constrained area, as they were collected from well understood beds in a succession. The careful and extensive sampling has allowed for the reconstruction of many plants, including platanaceous and cercidiphyllous plants, which are similar to those found in other localities, but not identical. These careful

reconstructions facilitate a detailed understanding of the floras of the many sub-environments of the Paleocene swamp and surrounding are floras. However, because they are from such a limited geographic area, there is less diversity than in other localities. For example, this flora is lacking many of the mesic remains found in other localities, like *Mesocyparis borealis*, reflecting the environment of swamps and meandering river deposits. They are also lacking the *Nelumbago* beds that are present at other localities, but which are not suspected of being in the typical swamp environment.

6.2.5 Genesee Locality (Chandrasekharam 1974)

This study has 19 species. However, it is unclear how many would be considered now. Many are leaf taxa of types that have been reinterpreted since 1974, often more than once. "Cercidiphylloids", *Azolla*, *Metasequoia* are the most common elements, but *Glyptostrobus*, *Ettingshausenia*, *Archeampelos* and plants included in the synonymy of *Browneia* are also present.

The Genesee locality is comparable to the current study area because much of the material is more poorly preserved than many localities. The Genesee locality most closely resembles area US 830 of the current study, which is much more *Metasequoia* and "Cercidiphylloid" dominated than the other localities in the current study. The association of *Azolla schopfii* with this flora in the Genesee locality is different than the association in the Big Muddy Valley, where it is found only in beds dominated by *Mesocyparis*. However, given that *A. schopfii* was found with a third, entirely distinct set of plants at Ravenscrag Butte, the determinism of environment through the presence of *A. schopfii* needs to be considered only with great care. It is unclear whether the roots present in beds of locality US 830 from the Big Muddy Valley were also found at the Genesee locality. If they were, it would help explain the differences in depositional environment that gave rise to this flora that is slightly different from all of the other floras of the Western Interior. *Metaseqoia* dominance is more common in Arctic floras of the time (Basinger 1991; McIver and Basinger 1999), so this difference in flora may be because it is far enough north to have light play a more important role in floral composition.

Despite their differences, the floras of the Big Muddy Valley and the Genesee locality share many members. The Genesee locality, although slightly abarent in content, is much more typical of the northern type floras, with higher conifer content compared to localities further south. The dominant floral elements in the Genesee locality and the Big Muddy Valley are found in numerous localities to the south of the Big Muddy Valley, but their dominance is less in localities south of the Big Muddy Valley and replaced by a more complex angiosperm flora.

6.2.6 Fort Union Formation (Johnson 2002)

This study produced 85 morphotypes, 33 with binomials. It is difficult to compare the Fort Union flora with that of the present study as it uses a non-traditional taxonomic system. There is a possibility that the 52 morphotypes without binomials may represent subsections of more inclusive taxa represented in other studies. The goal of morphotyping is not to sort out the full range of variability for the taxa, and fully recognizes that many of the morphotypes reflect different morphologies of leaves from the same species. For example, two leaves that were otherwise identical that varied from one another by the presence or absence of teeth would be considered different morphotypes. However, for climate analysis, these narrower subsets with distinctive characteristics are ideal, as they provide a better base for consideration of floral leaf characters. Distinguishing complex taxa with extensive variability is a difficult undertaking, and adds ambiguity to the results when doing this climate analysis. A taxon that is described as having both complete margins and toothed margins, such as *Zyziphoides flabella* or *Cornophyllum newberryi*, cause difficulties in climate analysis, as the presence of teeth is often considered an important character for climate analysis in the Northern Hemisphere (Wolfe 1993; Wolfe and Spicer 1999). An account that specifies only the species in a list would not reflect the status of this trait, whereas having morphotypes would allow the traits of each leaf collected to be considered more quickly in analysis. More work needs to be done bridging the morphotype/binomial barrier that exists, but such an undertaking will be long and difficult.

6.2.7 Denver Basin (Barclay et al. 2003)

This study produced 49 morphotypes, 16 (21) with binomials. The floral composition is similar to other earliest Paleocene locations, such as the Ravenscrag Butte Flora and the Fort Union Floras of the Williston. It is angiosperm-dominated, with only one bed being conifer dominated, and pteridophytes are minor elements. Like most of the earliest Paleocene floras, the most common elements are swamp elements, and are widely distributed and common in many localities. However, many of the taxa are rather different than most of the northern localities, as evidenced by the lack of conifer dominance. Platanoids are absent from this flora. Instead, it contains a higher percentage of the cornaceous taxa, such as *Browniea* and *Cornophyllum*. This study helps illustrate the conclusion reached by McIver and Basinger (1993), where they stated that the Ravenscrag Butte flora occurs at an ecotone between the more southerly floras and the arctic floras. The flora of the current study also follows this interpretation, largely consisting of the same elements as the Ravenscrag Butte flora, but with small variations. These variations largely are rare elements in the Big Muddy flora, and are representative of taxa more commonly found to the south. Few taxa are unique to the Ravenscrag Formation, instead, it shows a mix of more northerly floras like the Smokey Tower or Joffre Bridge Roadcut and more southerly floras like the one from the Denver Basin.

6.2.8 Fort Union Formation (Brown 1962)

This monograph is a posthumous collection of R. W. Brown's extensive studies on Paleocene floras, including notes on approximately 170 species and covers the entirety of the Western Interior. The taxonomy of this monograph is currently under revision (Manchester and Hickey 2007; Manchester 1999), as it represents a culmination of the old taxonomy of the region. Typical methodologies of old Paleocene palaeobotany typically utilized a "picture matching" methodology, where fossil leaves were compared to extant leaves, and generic assignment was usually applied through similarity. Recent opinion holds that it is likely that the majority of these leaves do not belong to modern genera, and instead achieve their similarity due to convergence.

This exhaustive monograph includes nearly all of the fossils found in the current study. Only a few species are not represented, particularly *Harmsvernia* and the unknowns, as well as possibly *Fagopsiphyllum praegroenlandicum*. *F. groenlandicum* is represented, so *F. praegroenlandicum* specimens easily could have been mixed into that collection (Berry 1935). Of note on the thoroughness of this monograph, many species found in the current study are found in this monograph but not in the other monographs published after 1900, including Berry's monograph, which as mentioned above specifically dealt with the area around the Big Muddy Valley. There is some indication of the distribution of plants, but this is not considered equally throughout the document, so the sub-floras or distinct floras that are present across the Western Interior are not distinct. Instead, the 170 species become considered a single entity, with little indication of the sub-environments. Some of the diverse floras are correlated to localities, but it is difficult to ascertain this information from this monograph.

6.2.9 Almont locality, Fort Union Formation (Crane et al. 1990)

The Almont locality is a middle Paleocene locality from North Dakota featuring 30 kinds of fruit, six kinds of inflorescences/flowers, 24 types of leaves. The floral make up of the Almont locality is different from the Big Muddy Valley. The flora of the Big Muddy Valley is more conifer dominated, whereas the Almont flora is restricted to *Parataxodium* for conifer content.

The Almont flora preserves permineralized fruiting bodies, unlike most of the floras of the Western Interior, as well as associated foliage. This allows for anatomical comparisons between these fossils and the extant, so more accurate designations can be made. Associations between the leaves and the fruits can be made, so that leaf and limited fruit impressions found elsewhere can be accurately understood and put into proper context. In addition to preserving anatomy, these specimens exhibit an overall high quality of preservation.

The Almont flora has been instrumental in reinterpreting the taxonomy of the Paleocene floras from many localities. Many of the taxonomic changes, such as the recognition of *Zyziphoides flabella* and *Nordenskioldia borealis* as part of the Trochodendraceae, originated in the Almont collection. The exceptional preservation

and large collection of reproductive materials allows the complete interpretation of specimens found in other localities which exhibit poor preservation. However, it has only been of use in relatively few of the cases with the flora of the Big Muddy Valley. *Browniea*, *Davidia*, *Nordenskioldia* and *Nyssidium* have benefited from understandings gleaned from the Almont locality, but in general, the Almont flora is more typical of the flora of localities to the south of the Big Muddy Valley.

6.2.10 Golden Valley Formation (Hickey 1977)

Two units are recognized in the Golden Valley Formation, the Bear Den Member which is latest Paleocene in age, and the Camels Butte Member, which is earliest Eocene in age. There are 41 species recognized in the Bear Den Member, and 34 species recognized in the Camels Butte Member. There is more similarity between the Bear Den Member sub-flora and the sub-floras of the Big Muddy Valley than between the Camels Butte sub-flora and the subfloras of the Big Muddy Valley. This makes sense, as there is a recognizable shift in floras at the Eocene boundary, which is one of the indicators of the epoch shift. This shift seems at least partially associated with the Paleocene-Eocene Thermal Maximum, a period of intense global warming that occurred at the time of the boundary (Wing et al. 2005). This brief period produces a distinct flora from both the Late Paleocene and Early Eocene sub-floras, both of which are more equitable in climate. Climate interpretations of all of the periods are warmer than the earliest Paleocene. Additionally, although the world is interpreted as overall more consistent in temperature, the present study is further north than these floras. Sub-flora 3 is the nearest in both age and distance to the Golden Valley Formation localities. Unfortunately, sub-flora 3 represents a different environment than the swamp flora preserved in virtually all other Western Interior localities, including the ones in the study of the Golden Valley Formation.

The climate change, latitudinal change and general species succession help explain the flora differences between the floras of the present study and the Bear Den Member; however latitudinal differences likely played only a minimal role, as these floras are closer geographically than many of the other floras considered, although they do illustrate the variation that occurs close to the latitude of the current study and those

nearby to the south. Climate and floral change are likely closely related, although it seems many of the Paleocene taxa are on the way out already. *Mesocyparis borealis* and *Paranymphaea crassifolia* are definitely not known to persist after the end of the Paleocene, and although they are regionally rare members of even the Early Paleocene, they are rarer in the late Paleocene. The massive climate change causes the floras adapted to the cooler Early Paleocene climes to retreat towards the poles, where the members not able to adapt to the unique conditions go extinct.

6.2.11 Isle of Mull (Boulter and Kvacek 1989)

This flora is the most distant geographically from the other floras. They are all part of the Western Interior of North America, whereas this one is part of the Brito-Arctic Igneous Province (BIP), a large zone covering Svarbald, eastern Greenland, and the western British islands primarily, although it has floral links to the rest of the arctic (Boulter and Kvacek 1989). The composition of the arctic floras plays a large role in the composition of the Ravenscrag floras, which exist in the suspected southern end of the Arctic province.

These BIP floras occur within the Paleocene as well, albeit the late Paleocene and Early Eocene instead of the Early to Middle Paleocene. This makes them most relevant for comparison with the Golden Valley Formation localities chronologically. However, they are more similar latitudinally to the Ravenscrag floras. Sub-flora 2 and sub-flora 3 of this flora are both latitudinally and chronologically similar. However, these sub-floras are more dissimilar to the Isle of Mull flora than sub-flora 1 is. No *Mesocyparis* sp. has been found in the Isle of Mull flora, although the same genera of all the other elements of sub-flora 2 are reported from Mull. The elements of sub-flora 3 are not represented in Mull, but this is likely due to sub-flora 3 representing a facies that is not commonly preserved, given that it is not known from any other study either.

The flora of the Isle of Mull is at least superficially similar to the flora considered in the present study. The taxa present in both of these studies are similar, including Platanoids (the taxonomy of the *Platanus* in the Mull study is likely out of date, and it may also be *Ettingshausenia*), *Cercidiphyllum*, *Metasequoia*, *Onoclea*, *Glyptostrobus* and *Fagopsiphyllum* amongst others. However, many of the species are

different. It is unclear whether this difference is due to regional taxonomic bias, as some of the taxa are under debate between North American and European considerations (*Dennstaedtia americana* vs *Dennstaedtia blomstrandii* for example), or whether this accurately reflects the natural species variation.

6.2.12 Koryak Upland (Golovneva 1994)

Up to 100 species have been identified in the Koryak Upland Basin floras, which consist of plants from the Maastrichtian and Early Paleocene Rarytkin Formation, Kakanaut Formation and Koryak Formation. For comparative purposes, the upper Rarytkin Formation and Koryak Formation are more interesting for comparison with the Big Muddy Valley, as these are the ones that are dated to Early Paleocene in age.

When interpreted so the taxonomies match, the Rarytkin episode, which includes the Early Paleocene floras, closely resembles the floras present in the Big Muddy Valley. Both sub-flora 1 and sub-flora 2 are well represented, with the members of both sub-floras being relatively common. The Koryak Upland upper flora includes some *Mesocyparis* beds, which is a feature that is shared between the Ravenscrag Formation and the Koryak Uplands. These features are not shared with the majority of floras found between the Ravenscrag Formation floras, and the Big Muddy flora in particular, and the Koryak Upland floras.

Despite the similarities, the Big Muddy Valley floras have many differences as well. Sub-flora 3 is not present in the Koryak floras. Other strictly North American elements, such as *Paranymphaea* and *Paloreodoxites* are also absent. The absent species are primarily found further south, with the Ravenscrag floras offering the northern limit of their range.

Overall, the Koryak Upland floras, when compared to the Mull floras (Boulter and Kvacek 1989) and knowledge of the Canadian Arctic floras (McIver and Basinger 1999) provide an understanding of the common Arctic flora of the Paleocene. This flora, with its high percentage of ferns and conifers, is present in all localities north of the Ravenscrag formation, although its complete dominance does not occur till after the Arctic Circle. Of the Arctic flora subsets, the Big Muddy Valley shares the most in common with the Koryak floras.

6.2.13 Overall Interpretation

The floral composition of the current study is both consistent with other Paleocene floras of the Northern Hemisphere but also distinct in specific ways. Sub-flora 1, which is a back swamp sub-flora of the greater flora, is similar to other localities. However, it is conifer-rich by specimen amounts. Angiosperm specimens are rare elements overall. This is similar to the Smokey Tower locality, but not consistent with many of the other localities, which may be conifer-rich, but still produce adequate woody angiosperm specimens to run multivariate climate interpretations. That was not the case with this study area, where the most diverse localities would produce at most 10 varieties of angiosperm, often incomplete and poorly preserved. Pteridophytes are rather diverse in the study area compared to the other localities, although there was a sampling bias towards them, as Mr. Larson intentionally collected ferns whenever possible (A. Larson, personal communication 2005). This resulted in 25% of the recognized diversity of the Big Muddy Valley being pteridophytes.

The flora of the Big Muddy Valley is a transitional flora between the arctic forests, which feature a large conifer content and share many characters around the pole and the angiosperm dominated floras to the south. Though only a sampling of localities were taken in comparison from further north in the preceding section, the flora is at these localities to those found elsewhere around the pole (McIver and Basinger 1999). In the transitional zone, a mix of both forest types occurs, although it more closely resembles the arctic flora for the most part. However, the relative abundances are different from the localities to the north and south. *Glyptostrobus* appears in all of the floras to the north and south, as does *Metasequoia*, *Zyziphoides*, *Cercidiphyllum* and various Platanaceae, although these elements make larger percentages of more northerly floras than those to the south.

The species from the warmer climates largely form rare elements of this flora. The abundance of these elements, which are mainly angiosperms, grows greater in the north-south transect going south. Tropical elements, including leaves with drip tips and palms, become more common as floras are explored to the south. The Big Muddy flora occurs near the ecotone shift between the polar broadleaf deciduous forests and those of

warmer climates. Part of this is shown by the change in composition in localities to the south, which have different ratios of composition. There are more angiosperms, especially entire margined leaves, to the south. The woody angiosperms of the Big Muddy Valley flora are all toothed except one poorly understood specimen.

The Cretaceous-Tertiary boundary exhibits what is considered a local minimum in palaeotemperature, although estimates still place it much higher than today (Johnson 2002). The heating that occurs throughout the Paleocene to reach a maximum at the Paleocene-Eocene (Wing et al. 2005) means that these floral elements shift further north. This shift causes the floras of this type to be found primarily further north. Recent explorations consider that this type of flora is reflective of the Arctic province during the late Cretaceous and Paleogene, moving southwards during cooling climates, when temperature regimes of the mid and low latitudes matched those previously restricted to polar regions. This is reflected in the later distribution of these floras, which covered what are now the temperate zones during the Neogene. Due to the higher temperatures and moisture of the Paleogene, the elements of this flora became isolated to subtropical refugia, as they exhibit nearly the same climate parameters (McIver and Basinger 1993). Despite being poorly preserved, the diversity documented in the Big Muddy Valley flora provides evidence for a mixed transitional flora between the Arctic floras and the floras of the numerous basins of the Western Interior of the United States. The mix of taxa in the present study illustrates this well, establishing the northern limit for many taxa, and being one of the most southerly localities with clear conifer dominance.

CHAPTER 7
CONCLUSIONS

The Ravenscrag Formation beds of the Big Muddy Valley area within the Willow Bunch Lake map area (72H) of southern Saskatchewan, Canada contain many beds that produce plant fossils. These beds range in age from earliest earliest Paleocene, (approximately 65.5 million years ago) to the P4 zone of Demchuck (1990), which is early Late Paleocene (approximately 58 million years ago).

Forty different species of plants were recognized in the current collections, consisting of 10 pteridophytes, 7 conifers, and 23 angiosperms. One new generic name, *Harmsvernia*, is proposed to replace *Harmsia* McIver and Basinger, an invalid genus, and thereby create the new combination *Harmsvernia hydrocotyloidea* (McIver and Basinger) comb. nov., and one new genus is established for remains of a taxodioid conifer, *Corvirupestrobus*, and the new species *Corvirupestrobus adrielensis* gen. et sp. nov. is created. A new species of the coniferous genus *Elatocladus* is established, *Elatocladus megasequoiae* sp. nov. Many of the other species are new to the Ravenscrag Formation. Two additional new combinations are also recognized. *Quercus praegroenlandicum* Berry is transferred to *Fagopsiphyllum praegroenlandicum* (Berry) comb. nov., and *Lastrea goldianum* auct. non (Lesquereux) Lesquereux is transferred to *Thelypteris* sp.

The flora exhibits three distinct sub-floral assemblages. The first sub-flora resembles other Paleocene localities in theWestern Interior, such as those found at Ravenscrag Butte (McIver and Basinger 1993), Joffre Bridge (Hoffman 2002), and Smokey Tower (Christophel 1976), as well as various localities from the Fort Union Formation of Montana and North Dakota (Brown 1962; Crane et al. 1991; Johnson 2002). It is largely a *Glyptostrobus*-dominated lowland and swamp flora, with numerous subenvironments represented, mostly from P1 to P2 zone in age. The second sub-flora is a *Mesocyparis*-dominated flora, likely representing a drier environment in the floodplain, of early P4 age. The third sub-flora is dominated by *Carya antiquorum* with little conifer content, of late P4 in age.

Paleoenvironmentally, the study area appears to have been primarily a swampy lowland forest occurring on the floodplain of a meandering river system. The water table was high most of the time, facilitating widespread coals. However, ironstone beds show that this was frequently disrupted. Sediment source is interpreted as coming from the cordillera to the northwest. Sediment is typically fine grained to sandy, owing at least partially to the distance the study area lies from the sediment source, as well as the forested landscape functioning to slow the fluvial system.

The paleoclimate has been interpreted to have been humid USDA hardiness zone 8. This was determined primarily through a modification of the Coexistance Approach (CA), but is supported by the presence of coals and crocodiles, as well as through the climate determination of other studies in the Western Interior. Application of climatological methods using leaf physiogamy could not be adequately applied to these localities due to a lack of woody angiosperms, as many of the key species are not present in available CA databases.

The Big Muddy Valley area exhibits a flora that is transitional between the polar conifer and broadleaf deciduous forests to the north and evergreen forests to the south. The primary factor dictating the transition between the forest zones seems to be light, as floral and faunal composition to the north and south suggest comparable moisture levels and temperature. This fits with the estimated paleolatitude of about 55° North. The sub-floras indicate that the Big Muddy Valley's paleoflora occurred at an ecotone, with mixed elements more typical of forests to the north or to the south. This floral composition is unique to the Big Muddy Valley. Of other reported Paleocene floras, the flora of the Big Muddy Valley is most similar overall to the flora of Ravenscag Butte, which is present in the Ravenscrag Formation in southwest Saskatchewan and P1 to P3 in age (McIver and Basinger 1993). The most common floral elements from both of these areas are the same. However, the rare elements differ, in particular sub-flora 2 and sub-flora 3 are not represented at Ravenscrag Butte. Other Paleocene floras from farther north contain floras that resemble sub-flora 2, and Paleocene floras from farther south contain floras that resemble sub-flora 3. Therefore, this study offers insights into a transitional flora during a well studied and important time in Earth history, from when the forests were recovering from the K-T event towards the Eocene thermal maximum.

REFERENCES

Note: This reference list encompasses the main text as well as the appendices.

Alvarez, L. W., W. Alvarex, F. Asaro, and H. V. Michel. (1980). "Extraterrestrial cause for the Cretaceous Tertiary extinction." Science 4448: 1095-1108.

Alvin, K. L., and M. C. Boulter. (1974). "A controlled method of comparative study for Taxodiaceous leaf cuticles." Bot. J. Linn. Soc. 69: 277-286.

APG-II. (2003). "An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II." Bot. J. Linn. Soc. 141: 399-436.

Aulenback, K. R., and B. A. LePage. (1998). "*Taxodium wallisii* sp. nov.: First occurrence of *Taxodium* from the upper Cretaceous." Int. J. Plant Sci. 159: 376-390.

Barclay, R. S., K. R. Johnson, W. J. Betterton, and D. L. Dilcher (2003). "Stratigraphy, megaflora, and the K-T boundary in the eastern Denver Basin, Colorado." Rocky Mountain Geology 38: 45-71.

Basinger, J. F. (1991). “The fossil forests of the Buchanan Lake Formation (Early Tertiary), Axel Heiberg Island, Canadian Arctic Archipelago: preliminary floristics and paleoclimate.” *In* Christie, R L. and N.J. McMillan (eds.). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geol. Surv. Canada, Bull. 403: 39-65.

Basinger, J. F., D. R. Greenwood, and T. Sweda (1994). “Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation.” *In* Boulter, M. C. and H. C. Fisher (eds.). Cenezoic Plants and Climates of the Arctic. Berlin Heidelberg, Springer-verlag NATO ASI Series, vol. 27: 175-198

Bell, W. A. (1949). “Uppermost Cretaceous and Paleocene Floras of Western Alberta.” Geol. Surv. Canada, Bull. 13: 1-231.

Bell, W. A. (1957). "Flora of the upper Cretaceous Nanimo Group of Vancouver Island, British Columbia." Geol. Surv. Canada, Mem. 293: 1-84.

Berry, E. W. (1916). "The lower Eocene floras of southeastern North America." US Geol. Surv. Prof. Pap. 91.

Berry, E. W. (1930). "Fossil plants from the Cypress Hills of Alberta and Saskatchewan." National Museums of Canada, Bulletin 63: 15-28.

Berry, E. W. (1934). "A lower Lance florule from Harding County, South Dakota." US Geol. Surv. Prof. Pap. 185 F: 127-133.

Berry, E. W. (1935). "A preliminary contribution to the floras of the Whitemud and Ravenscrag Formations." Geol. Surv. Canada, Mem. 182: 1-107.

Boulter, M. C., and Z. Kvacek. (1989). "The Palaeocene flora of the Isle of Mull." Spec. Pap. Palaeontol. 42: 1-149.

Bown, T. M., K. D. Rose, E. L. Simons, and S. L. Wing. (1994). “Distribution and stratigraphic correlation of upper Paleocene and lower Eocene fossil mammal and plant localities of the Fort Union, Willwood, and Tatman Formations, southern Bighorn Basin, Wyoming.” US Geol. Surv. Prof. Pap. 1540.

Boyd, A. (1992). “Revision of the Late Cretaceous Pautût flora from west Greenland: Gymnospermopsida (Cycadales, Cycadeoidales, Caytoniales, Ginkgoales, Coniferales).” Palaeontogr. Abt. B 225: 105-172.

Braman, D. R., and A.R. Sweet. (1999). "Terrestrial palynomorph biostratigraphy of the Cypress Hills, Wood Mountain, and Turtle Mountain areas (upper Cretaceous - Paleocene) of western Canada." Can. J. Earth Sci. 36: 725-741.

Braman, D. R., A. R. Sweet, and J. F. Lerbekmo. (1999). "Upper Cretaceous-lower Tertiary lithostratigraphic relationships of three cores from Alberta, Saskatchewan, and Manitoba, Canada." Can. J. Earth Sci. 36: 669-683.

Broughton, P. L. (1977). "Origin of coal basins by salt solution." Nature 270: 420-423.

Broughton, P. L. (1978). Willow Bunch Map-Area. *In* S. H. Whitaker (ed.). Coal resources of southern Saskatchewan: a model for evaluation methodology. Geol. Surv. Canada, Ec. Geol. Report 30: 69-79.

Brown, R. W. (1936). "The genus *Glyptostrobus* in America." Washington Acad. Sci. Jour. 26: 353-357.

Brown, R. W. (1939). "Some American fossil plants belonging to the Isoetales." Washington Acad. Sci. Jour. 29: 261-269.

Brown, R. W. (1956). "New items in the Cretaceous and Tertiary floras of the Western United States." Washington Acad. Sci. Jour. 46: 103-108.

Brown, R. W. (1962). "Paleocene flora of the Rocky Mountains and Great Plains." US Geol. Surv. Prof. Pap. 375.

Brunsfeld, S. J., P. E. Soltis, D. E. Soltis, P. A. Gadek, C. J. Quinn, D. D. Strenge, and T. A. Ranker. (1994). "Phylogenetic relationships among the genera of Taxodiaceae and Cupressaceae: evidence from rbcL sequences." Syst. Bot. 19: 253-262.

Butala, J. R., and A. A. Cridland. (1978). "Nomenclature of fossil *Glyptostrobus* in North America." Taxon 27: 15-20.

Catuneanu, O., and A. R. Sweet. (1999). "Maastrichtian-Paleocene foreland-basin stratigraphies, western Canada: a reciprocal sequence architecture." Can. J. Earth Sci. 36: 685-703.

Catuneanu, O., A. R. Sweet, and A. D. Miall. (2000). "Reciprocal stratigraphy of the Campanian-Paleocene Western Interior of North America." Sed. Geol. 134: 235-255.

Chandrasekharam, A. (1974). "Megafossil flora from the Genesee locality, Alberta, Canada." Palaeontogr. Abt. B 147: 1-41.

Chaney, R. W. (1951). "A revision of fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*." Trans. Am. Phil. Soc. New series 40: 172-239.

Christophel, D. C. (1976). "Fossil floras of the Smokey Tower Locality, Alberta, Canada." Palaeontogr. Abt. B 157: 1-43.

Colbert , L. H., R. B. Cowles, and C. M. Bogert. (1946). "Temperature tolerances in the American alligator and their bearing on the habitats, evolution and extinction of the dinosaurs." Amer. Mus. Natural Hist. Bull. 36: 330-373.

Collinson, M. E. (2001). "Cainozoic ferns and their distribution." Brittonia 53: 173-235.

Crane, P. R. (1984). "A re-evaluation of *Cercidiphyllum*-like plant fossils from the British Early Tertiary." Bot. J. Linn. Soc. 89: 199-230.

Crane, P. R., and R. A. Stockey. (1985). "Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the late Paleocene of Alberta, Canada." Can. J. Bot. 63: 340-364.

Crane, P. R., S. R. Manchester, and D. L. Dilcher. (1990). "A preliminary survey of fossil leaves and well preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont North Dakota." Fieldiana: Geology New Series 20: 1-59.

Crane, P. R., S. R. Manchester, and D. L. Dilcher. (1991). "Reproductive and vegetative structure of Nordenskioldia (Trochodendraceae), a vesselless dicotyledon from the Early Tertiary of the Northern Hemisphere." Am. J. Bot. 78: 1311-1334.

Daly, D. J., C. R. Schmit, and M. A. Sholes. (1990). "A review of the geology and depositional environments of the coal-bearing sequence in the Fort Union lignite region. Geology and utilization of Fort Union lignites." *In* R. B. Finkelman, S. J. Tewalt, and D. J. Daly, eds. Geology and utilization of Fort Union lignites. Environmental and Coal Associates: 3-51.

Davies-Vollum, K. S., and S. L. Wing. (1998). "Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming)." Palaios 13: 28-40.

Dawson, F. M., C. G. Evans, R. Marsh, and R. Richardson. (1994). "Uppermost Cretaceous and Tertiary Strata of the Western Canadian Sedimentary Basin". *In* Mossop, G. D., and I. Shetson (comp.). Geological Atlas of the Western Canada Sedimentary Basin. Calgary, Alberta: Canadian Society of Petroleum Geologists and Alberta Research Council.

Dawson, J. W. (1883). "On the Cretaceous and Tertiary floras of British Columbia and the Northwest Territory." Trans. Royal Soc., Canada (sec. 4) 1: 15-34.

Dawson, J. W. (1887). "On the fossil plants of the Laramie Formation of Canada." Trans. Royal Soc., Canada (sec. 4) 4: 19-34.

Day, F. P. (1982). "Litter decomposition rates in the seasonally flooded Great Dismal Swamp." Ecology 63: 670-678.

Demchuck, T. D. (1990). "Palynostratigraphic zonation of Paleocene strata in the central and south-central Alberta Plains." Can. J. Earth Sci. 27: 1263-1269.

Diemer, J. A., and E. S. Belt. (1991). "Sedimentology and paleohydraulics of the meandering rivers systems of the Fort Union Formation, southeastern Montana." Sed. Geol. 75: 85-108.

Dijkstra, S. J. (1961). "Some Paleocene megaspores and other small fossils." Mededelingen van de Geologische Stichting Nieuwe Serie 13: 5-11.

Dilcher, D. L. (1969). "Podocarps from the Eocene of North America." Science 164: 299-301.

Eberle, J. J., and J. E. Storer. (1999). "Northernmost record of brontotheres, Axel Heiberg Island, Canada --- Implications for age of the Buchanan Lake Formation and brontotheres." J. Paleont. 73: 979-983.

Eckenwalder, J. E. (1976). "Re-evaluation of Cupressaceae and Taxodiaceae: A proposed merger." Madroño 23: 237--256.

Ellis, B., K. R. Johnson, and R. E. Dunn. (2003). "Evidence for and *in situ* Early Paleocene rainforest from Castle Rock, Colorado." Rocky Mountain Geology 38: 73-100.

Fairon-Demaret, M., J. Hilton, and C. M. Berry. (1999). Surface preparation for macrofossils (degagement). *In* Jones, T. P., and N. P. Rowe (eds). Fossil Plants and Spores: Modern Techniques. London, Geological Society: 31-33.

Farjon, A. (2005.). A monograph of Cupressaceae and *Sciadopitys*. Kew, Royal Botanic Gardens.

Fraser, F. J., F. H. McLearn, L. S. Russel, P. S. Warren, and R. T. D. Wickenden. (1935). "Geology of southern Saskatchewan." Geol. Surv. Canada, Mem. 176.

Frank, M. C., and S. L. Bend. (2004). "Peat-forming history of the ancestral Souris mire (Palaeocene), Ravenscrag Formation, southern Saskatchewan, Canada." Can. J. Earth Sci. 41: 307-322.

Furnival, G. M. (1946). "Cypress Lake map area." Geol Surv. Canada, Mem. 242.

Gadek, P. A., D. L. Alpers, M. M. Heslewood, and C. J. Quinn. (2000). "Relationships within Cupressaceae *sensu lato*: a combined morphological and molecular approach." Am. J. Bot. 87: 1044-1057.

Gardner, J. S. (1883-1886). "A monograph of the British Eocene Flora 2." Palaeontogr. Soc. (Monogr.): 1-159.

Gemmill, C. E. C., and K. R. Johnson. (1997). "Paleoecology of a Late Paleocene (Tiffanian) megaflora from the Northern Great Divide Basin, Wyoming." Palaios 12: 439-448.

Golovneva, L. B. (1994) The flora of the Maastrichtian-Danian deposits of the Koryak Upland of the northeast Russia. Cretaceous Reseach 15: 89-108.

Graham, A. (1999). Late Creatceous and Cenezoic history of North America vegetation, north of Mexico. Oxford University Press.

Hartman, J. H., and A. J. Kihm. (1990). Chronostratigraphy of Paleocene strata in the Williston Basin. Geology and utilization of Fort Union lignites. *In* R. B. Finkelman, S. J. Tewalt, and D. J. Daly (eds.). Geology and utilization of Fort Union lignites. Environmental and Coal Associates: 52-75.

Hartman, J. H., and J. I. Kirkland. (2002). Brackish and marine mollusks of the Hell Creek Formation of North Dakota: Evidence for a persisting Cretaceous seaway. *In* Hartman, J. H., K. R. Johnson, and D. J. Nichols (eds.). The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Boulder, Colorado, GSA Special Paper. 361: 271-296.

Heer, O. (1869). Flora fossilis alaskana, Kungl. Svenska Vetenskaps-akademiens Handlinger.

Heer, O. (1871). Die Miocene Flora und Fauna Spitzbergens, Kungl. Svenska Vetenskaps-akademiens Handlingar 8(7).

Hickey, L. J. (1977). "Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of Western North Dakota." GSA Memoir 150.

Hickey, L. J. (2001). "On the nomenclatural status of the morphogenera *Quereuxia* and *Trapago*." Taxon 50: 1119 - 1124.

Hicks, J. F., K. R. Johnson, J. D. Obradovich, D. P. Miggins, and L. Tauxe. (2003). "Magnetostratigraphy of Upper Cretaceous (Maastichtian) to lower Eocene strata of the Denver Basin, Colorado." Rocky Mountain Geology 38: 1-27.

Hicks, J. F., K. R. Johnson, J. D. Obradovich, L. Tauxe, and D. Clark. (2002). Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the age of the

Cretaceous-Tertiary boundary. *In* Hartman, J. H., K. R. Johnson, and D. J. Nichols (eds.). The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Boulder, Colorado, GSA Special Paper. 361: 35-55.

Hoffman, G. L. (2002). Paleobotany and paleoecology of the Joffre Bridge Roadcut locality (Paleocene), Red Deer, Alberta. Graduate Studies. Edmonton, University of Alberta. Masters of Science (Second Edition): 1-122.

Hoffman, G. L., and R. A. Stockey. (1994). "Sporophytes, megaspores and massulae of *Azzola stanleyi* from the Paleocene Joffre Bridge locality, Alberta." Can. J. Bot. 72: 301-308.

Hoffman, G. L., and R. A. Stockey. (1999). "Geological setting and paleobotany of the Joffre Bridge Roadcut fossil locality (Late Paleocene), Red Deer Valley, Alberta." Can. J. Earth Sci. 36: 2073-2084.

Hudson, J. H. (1987). "Recent studies on Saskatchewan Clays." *In* Gilboy, C. F., and L. W. Vigrass (eds.). Economic minerals of Saskatchewan. Saskatchewan Geological Society, Special Publication 8.

Iljinskaja, I. A. (1974). "*Trochodendroides* Berry, *Nyssidium* Heer." *In* Takhtajan, A. (ed.). Magnoliaphyta fossilia U.R.S.S., I, Magnoliaceae-Eucomiaceae. Leningrad, Nauka: 15-24.

International Code of Botanical Nomenclature (Vienna Code). (2006). Regnum Vegetabile 146. A.R.G. Gantner Verlag KG.

Jain, R. K., and J. W. Hall. (1969). "A contribution to the Early Tertiary fossil record of the Salviniaceae." Am. J. Bot. 56: 527-539.

Johnson, K. R. (1989). A high-resolution megafloral biostratigraphy spanning the Cretaceous-Tertiary boundary in the northern Great Plains, Yale. Doctor of Philosophy: 1-620.

Johnson, K. R. (1996). "Description of seven common fossil leaf species from the Hell Creek Formation (Upper Cretaceous: Upper Maastrichtian), North Dakota, South Dakota and Montana." Proc. Denver Mus. Nat. Hist. Series 3(12).

Johnson, K. R. (2002). "Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression." *In* Hartman, J. H., K. R. Johnson, and D. J. Nichols. (eds.). The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Boulder, Colorado, GSA Special Paper 361: 329-391.

Johnson, K. R., and B. Ellis. (2002). "A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary." Science 296: 2379-2383.

Johnson, K. R., M. L. Reynolds, K. W. Werth, and J. R. Thomasson. (2003). "Overview of the Late Cretaceous, Early Paleocene and Early Eocene megafloras of the Denver Basin, Colorado." Rocky Mountain Geology 38: 101-120.

Knowlton, F. H. (1910). "Description of fossil plants from the Mesozoic and Cenezoic of North America." Smithsonian Institution Miscellaneous Collections 52: 489-495.

Knowlton, F. H. (1917). "Fossil floras of the Vermejo and Raton formations of Colorado and New Mexico." US Geol. Surv. Prof. Pap. 101: 223-450.

Knowlton, F. H. (1930). "The flora of Denver and associated formations of Colorado; a posthumous work edited by E.W. Berry." US Geol. Surv. Prof. Pap. 155: 1-142.

Koch, B. E. (1963). "Fossil plants from the lower Paleocene of the Agatdalen (Angmârtussut) area, central Nûgssuaq peninsula, northwest Greenland." Grønlands Geologiske Undersøkelse Bulletin 38.

Kroeger, T. J., and E. N. Steadman. (1990). "Review of palynological research on Paleocene rocks of the Williston Basin. Geology and utilization of Fort Union lignites." *In* R. B. Finkelman, S. J. Tewalt, and D. J. Daly, (eds.). Geology and utilization of Fort Union lignites. Environmental and Coal Associates: 76-86.

Kryshtofovich, A. N. (1953). Some enigmatic plants of the Creataceous flora and their phylogentic significance. Paleontologiya i stratigrafiya. Moscow, State publishing house for Geological Literature.

Kvacek, Z., and S. R. Manchester. (1999). "Eostangeria Barthel (extinct Cycadales) from the Paleogene of western North America and Europe." Int. J. Plant Sci. 160: 621-629.

Kvacek, Z., and S. R. Manchester. (2004). "Vegetative and reproductive structure of the extinct *Platanus neptuni* from the Tertiary of Europe and relationships within the Platanaceae." Plant Systematics and Evolution 244: 1-29.

Kvacek, Z., S. R. Manchester, and S. X. Guo. (2001). "Trifoliate leaves of *Platanus bella* (Heer) comb. nov. from the Paleocene of North America, Greenland, and Asia and their relationships among extinct and extant Platanaceae " Int J. Plant Sci. 162: 441-458.

Kvacek, Z. and S. B. Manum. (1993). "Ferns in the Spitsbergen Palaeogene." Palaeontogr. Abt. B 230: 169-181.

Leaf Architecture Working Group (1999). Manual of Leaf Architecture morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms. Smithsonian Institute: 1-65.

LePage, B. A. (2007). "The Taxonomy and Biogeographic History of *Glyptostrobus* Endlicher (Cupressaceae)." *In* Yang, H., and L. J. Hickey (eds.). *Metasequoia*: Back from the Brink? An Update; Proceedings of the Second International Symposium on *Metasequoia* and Associated Plants August 6–10, 2006, Bulletin of the Peabody Museum of Natural History 48: 359-426.

Lerbekmo, J. F. (1985). "Magnetostratigraphic and biostratigraphic correlations of Maastrichtian to Early Paleocene strata between south-central Alberta and southwestern Saskatchewan." Bull. Can. Petrol. Geol.33: 213-226.

Lerbekmo, J. F. (1999). "Magnetostratigraphy of the Canadian Continenetal Drilling Program Cretaceous-Tertiary (K-T) Boundary Project core holes, western Canada." Can. J. Earth Sci. 36: 705-715.

Lerbekmo, J. F., A. R. Sweet, and R. A. Davidson. (1999). "Geochemistry of the Cretaceous-Tertiary (K-T) boundary interval: south-central Saskatchewan and Montana." Can. J. Earth Sci. 36: 717-724.

Lesquereux, L. (1874). "The lignitic formation and its fossil flora." US Geol. Surv. of the Territories, Annual Report (1873) 7: 365-425.

Lesquereux, L. (1883). "Contributions to the fossil floraof the Western Territories, Part 3, The Cretaceous and Tertiary floras." US Geol. Surv. of the Territories, Report 8: 1-283.

Liu, Y. J., C. S. Li, and Y. F. Wang. (1999). "Studies on fossil *Metasequoia* from north-east China and their taxonomic implications." Bot. J. Linn. Soc. 130: 267-297.

Lund, S. P., J. H. Hartman, and S. K. Banerjee. (2002). "Magnetostratigraphy of the interfingering Cretaceous-Paleocene marine continental strata of the Williston Basin, North Dakota and Montana." *In* Hartman, J. H., K. R. Johnson, and D. J. Nichols (eds.). The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Boulder, Colorado, GSA Special Paper. 361: 57-54.

Mack, G. H., and W. C. James. (1994). "Paleoclimate and the global distribution of paleosols." J. Geol. 102: 360-366.

Manchester, S. R. (1986). "Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America." Bot. Gaz. 147: 200-226.

Manchester, S. R. (1987). "Early history of the Junglandaceae." Pl. Syst. Evol. 162: 231-250.

Manchester, S. R. (1999). "Biogeographical relationships of North American Tertiary floras." Ann. Mo. Bot. Gard. 86: 472-522.

Manchester, S. R. (2001). "Leaves and fruits of *Aesculus* (Sapindales) from the Paleocene of North America." Int. J. Plant Sci. 162: 985-998.

Manchester, S. R. (2002). "Leaves and fruits of *Davidia* (Cornales) from the Paleocene of North America." Syst. Bot. 27: 368-382.

Manchester, S. R., M. A. Akhmetiev., and T. M. Kodrul. (2002). "Leaves and fruits of *Celtis aspera* (Newberry) Comb. Nov. (Celtidaceae) from the Paleocene of North America and eastern Asia." Int. J. Plant Sci. 163: 725-736.

Manchester, S. R., and Z. D. Chen. (1996). "*Palaeocarpinus aspinosa* sp. nov. (Betulaceae) from the Paleocene of Wyoming, U.S.A." Int. J. Plant Sci. 157: 644-655.

Manchester, S. R., and Z. D. Chen. (1998). "A new genus of Coryloideae (Betulaceae) from the Paleocene of North America." Int. J. Plant Sci. 159: 522-532.

Manchester, S. R., and P. R. Crane. (1983). "Attached leaves, inflorescences, and fruits of *Fagopsis*, an extinct genus of fagaceous affinity from the Oligocene Florissant flora of Colorado, U. S.A." Am. J. Bot. 70: 1147-1164.

Manchester, S. R., P. R. Crane, and D. L. Dilcher. (1991). "*Nordenskioldia* and *Trochodendron* form the Miocene of northwestern North America." Bot. Gaz. 152: 357-368.

Manchester, S. R., P. R. Crane, and L. B. Golovneva. (1999). "An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and eastern Asia." Int. J. Plant Sci. 160: 188-207.

Manchester, S. R., and D. L. Dilcher. (1997). "Reproductive and vegetative morphology of *Polyptera* (Juglandaceae) from the Paleocene of Wyoming and Montana." Am. J. Bot. 84: 649-663.

Manchester, S. R., and S. X. Guo. (1996). "*Palaeocarpinus* (extinct Betulaceae) form northwestern China: new evidence for Paleocene floristic continuity between Asia, North America and Europe." Int J. Plant Sci. 157: 240-246.

Manchester, S. R., and L. J. Hickey. (2007). "Reproductive and Vegetative Organs of *Browniea* gen. n. (Nyssaceae) from the Paleocene of North America." Int. J. Plant Sci. 168: 229-249.

Manchester, S. R., K. B. Pigg, and P. R. Crane. (2004). "*Palaeocarpinus dakotensis* sp. n. (Betulaceae: Coryloideae) and associated staminate catkins, pollen, and leaves from the Paleocene of North Dakota." Int. J. Plant Sci. 165: 1135-1148.

Markwick, P. J. (1994). "“Equability,” continentality and Tertiary “climate”: The crocodilian perspective." Geol. 22: 613-616.

Matsumodo, M., T. A. Ohsawa, M. Nishida, and H. Nishida. (1997). "*Glyptostrobus rubenosawaensis* sp. nov., a new permineralized conifer species from the Middle Miocene, Central Hokkaido, Japan." Paleont. Res. 1: 81-99.

McIntyre, D. J. (1991.). “Pollen and spore flora of an Eocene forest, eastern Axel Heiberg Island, N.W.T”. *In* Christie, R. L., and N.J. McMillan (eds). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geol. Surv. Canada, Bull. 403: 83-98.

McIver, E. E. (1992). "Fossil *Fokienia* (Cupressaceae) from the Paleocene of Alberta, Canada." Can. J. Bot. 70: 742-749.

McIver, E. E., and K. R. Aulenback. (1994). "Morphology and relationships of *Mesocyparis umbonata* sp. nov.: fossil Cupressaceae from the Late Cretaceous of Alberta, Canada." Can. J. Bot. 72:: 273-295.

McIver, E. E. (1999). "Paleobotanical evidence for ecosystem disruption at the Cretaceous-Tertiary boundary from Wood Mountain, Saskatchewan, Canada." Can. J. Earth Sci. 36: 775-789.

McIver, E. E. (2002). "The paleoenvironment of *Tyrannosaurus rex* from southwestern Saskatchewan, Canada." Can. J. Earth Sci. 39:: 207-221.

McIver, E. E., and J. F. Basinger. (1987). "*Mesocyparis borealis* gen. et sp. nov.: fossil Cupressaceae from the Early Tertiary of Saskatchewan, Canada." Can. J. Bot. 65: 2338-2351.

McIver, E. E., and J. F. Basinger. (1989). "The morphology and relationships of *Equisetum fluviatoides* sp. nov. from the Paleocene Ravenscrag Formation of Saskatchewan, Canada." Can. J. Bot. 67: 2937-2943.

McIver, E. E., and J. F. Basinger. (1993). "Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada." Palaeontographica Canadiana 10: 1-167.

McIver, E. E., and J. F. Basinger. (1999). "Early Tertiary floral evolution in the Canadian High Arctic." Ann. Mo. Bot. Gard. 86: 523-545.

Miall, A. D. (1986). "The Eureka Sound Group (upper Cretaceous-Oligocene), Canadian Arctic Islands." Bulletin of Canadian Petroleum Geology 34: 240-270.

Miall, A. D. (1996). The Geology of Fluvial Deposits. Springer-Verlag.

Moiseeva, M. G. (2008). "New angiosperms from the Maastrichtian of the Amaam Lagoon area (northeastern Russia)." Paleontological Journal 42: 92–105.

Mosbrugger, V. (1999). “The nearest living relative technique.” *In* Jones, T.P. and N.P. Rowe (eds.) Fossil Plants and Spores: Modern Techniques. London, Geological Society: 261-266.

Mosbrugger, V., and T. Utescher. (1997). “The coexistence approach -- a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils.” Palaeogeography, Palaeoclimatology, Palaeoecology 134 : 61-86

Nambudiri, V. (1987). “Peat forming flora in the Paleocene Ravenscrag Formation, southern Saskatchewan.” University of Regina: Energy Research Unit Contribution 175.

Nanson, G. C. (1980). "Point bar and flood plain formation on the Beatton River, northeastern British Columbia, Canada." Sedimentology 27: 3-30.

Newberry, J. S. (1861). Fossil Plants. Reports upon the Colorado River of the West, Part 3. J. C. Ives. New York, Da Capo Press: 129-132.

Newberry, J. S. (1863). "Description of fossil plants collected by Mr. George Gibbs, geologist of the U.S. Northwest Boundary Commission under Mr. Archibald Campbell, U.S. Commissioner." Boston Journal of Natural History 7: 506-524.

Newberry, J. S. (1868). "Notes on the later extinct floras of North America with descriptions of some new species from the Cretaceous and Tertiary strata." N.Y. Lyc. Nat. Hist., Annals 9: 1-76.

Newberry, J. S. (1898). "The later extinct floras of North America." US Geol. Surv. Monograph 35.

Pabst, M. B. (1968). "The flora of the Chuckanut Formation-the Equisitales, Filicales , and Coniferales." University of California Publications in Geological Sciences 76: 1-85.

Paclt, J. (1997). "*Doliostrobus* (Araucariaceae) und *Glyptostrobus* (Taxodiaceae); analoge Etymologie zweier fossiler Gymnospermengattungen." Neues Jahrbuch fuer Geologie und Palaeontologie 7: 409-411.

Parizek, R. R. (1964). "Geology of the Willow Bunch Lake Area (72H) Saskatchewan." SRC Geology Division, Report no. 4.

Pearson, D. A., T. Schaefer, K. R. Johnson, D. J. Nichols, and J. P Hunter. (2002). "Vertebrate biostratigraphy of the Hell Creek Formation in southwestern North Dakota and northwestern South Dakota." *In* Hartman, J. H, K. R. Johnson, and D. J. Nichols (eds.). The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Boulder, Colorado, GSA Special Paper 361: 145-167.

Peppe, D. J., J.M. Erickson, and L.J. Hickey (2007). "Fossil leaf species from the Fox Hills Formation (Upper Cretaceous: North Dakota, USA) and their paleogeographic significance." J. Paleont. 81: 550-567.

Pigg, K. B., R. M. Dillhoff, M. L. DeVore, and W. C. Wehr. (2007). "New diversity among the trochodendraceae from the Early/Middle Eocene Okanogan Highlands of British Columbia, Canada, and northeastern Washington State, United States." Int. J. Plant Sci. 168: 521-532.

Pigg, K. B., and G. W. Rothwell. (2001). "Anatomically preserved *Woodwardia virginica* (Blechnaceae) and a new Filicalean fern from the Middle Miocene Yakima Canyon Flora of central Washington, USA." Am. J. Bot. 88: 777-787.

Pigg, K. B., and R.A. Stockey (1991). "Platanaceous plants from the Paleocene of Alberta, Canada." Rev. Pal. Pal. 70: 125-146.

Platt, N. H., and B. Keller. (1992). "Distal alluvial deposits in a foreland basin setting - the lower Freshwater Molasse (lower Miocene), Switzerland: Sedimentology, architecture and palaeosols." Sedimentology 39: 545-565.

Postnikoff, A. C. L., and J. F. Basinger. (2004). "Chinese swamp cypress (*Glyptostrobus*) in the fossil forests of Axel Heiberg Island, Nunavut, Canada." *In* Danby, R. K., H. Castleden, A.R. Giles, and J. Rausch (eds.). Breaking the Ice: Proceedings of the 7th (Inter)National Student Conference on Northern Studies. University of Alberta CCI Press, Edmonton: 131-140.

Potter, J., A. P. Beaton, W. J. McDougall, E. M. V. Nambudiri, and L. W. Vigrass. (1991). "Depositional evnvironments of the Hart coal zone (Paleocene), Willow Bunch Coalfield, southern Saskatchewan, Canada from petrographic, palynological, paleobotanical, mineral and trace element studies." Int. J. of Coal Geol. 19: 253-281.

Raynolds, R. G., and K. R. Johnson. (2003). "Synopsis of the stratigraphy and paleontology of the uppermost Cretaceous and lower Tertiary strata in the Denver Basin, Colorado." Rocky Mountain Geology 38: 171-181.

Read, R. W., and L. J. Hickey. (1972). "A revised classification of fossil palm and palm-like leaves." Taxon 21: 129-137.

Rees, P., M. T. Gibbs, A. M. Ziegler, J. E. Kutzbach, and P. J. Behiling. (1999). "Permian climates: Evaluating model predictions using global paleobotanical data." Geology 27: 891-894.

Reinink-Smith, L. M., and E. B. Leopold (2005). "Warm climate in the late Miocene of the south coast of Alaska and the occurrence of Podocarpaceae pollen." Palynology 29: 205-262.

Ricketts, B. D. (1986). "New formations in the Eureka Sound Group, Canadian Arctic Islands." Current Research, Part B, Geol. Surv. Canada, Pap. 86-1B: 363-374.

Ricketts, B. D. (1991). “Sedimentation, Eurekan tectonism and the fossil forest sucession on eastern Axel Heiberg Island.” *In* R. L. Christie, and N.J. McMillan (eds). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geol. Surv. Canada, Bull. 403: 1-28.

Rothwell, G. W., and R. A. Stockey. (1991). "*Onoclea sensibilis* in the Paleocene of North America, a dramatic example of structural and ecological stasis." Rev. Pal. Pal. 70: 113-124.

Schumm, S. A. (1977). The fluvial system. NY, Wiley.

Schweitzer, H. J. (1974). "Die "tertiaren" Koniferen Spitzbergens. [The "Tertiary" Conifers of Spitsbergen]." Palaeontogr. Abt. B 149: 1-89.

Smith, N. D., T. A. Cross, J. P. Dufficy, and S. R. Clough (1989). "Anatomy of an avulsion." Sedimentology 36: 1-23.

Smith, N. D., and M. Perez-Arlucea. (1994). "Fine-grained splay deposition in the avulsion belt of the lower Saskatchewan River, Canada." J. of Sed. Res. B 64: 159-168.

Spicer, R. A., A. B. Herman, and E. M. Kennedy. (2004). "Foliar Physiognomic Record of Climatic Conditions during Dormancy: Climate Leaf Analysis Multivariate Program (CLAMP) and the Cold Month Mean Temperature." J. Geol. 112: 685–702.

Stockey, R. A., G. L. Hoffman, and G. W. Rothwell. (1997). "The fossil monocot *Limnobiophyllum scutatum*: resolving the phylogeny of Lemnaceae." Am. J. Bot. 84: 355-368.

Stockey, R. A., and G. W. Rothwell. (1997). "The aquatic angiosperm *Trapago angulata* from the upper Cretaceous (Maastrichtian) St. Mary River Formation of southern Alberta." Int. J. Plant Sci. 158: 83-94.

Stockey, R. A., G. W. Rothwell, and A. B. Falder. (2001). "Diversity among taxodioid conifers: *Metasequoia foxii* sp. nov. from the Paleocene of Central Alberta, Canada." Int. J. Plant Sci. 162: 221-234.

Sun, F., and R. A. Stockey. (1992). "A new species of *Palaeocarpinus* (Betulaceae) based on infructescences, fruits, and associated staminate inflorescences and leaves from the Paleocene of Alberta, Canada." Int. J. Plant Sci. 153: 136-148.

Sweet, A. R. (1978). "Palynology of the Ravenscrag and Frenchman Formation. Coal resources of southern Saskatchewan: a model for evaluation methodology." *In* S. H. Whitaker (ed.). Coal resources of southern Saskatchewan: a model for evaluation methodology. Geol. Surv. Canada, Ec. Geol. Report. 30: 29-38.

Sweet, A. R. (1993). "Applied research report of 30 middle Paleocene samples from the Poplar River Mine (PitA3W), Willow Bunch area, Saskatchewan (LSD 4, sec. 15, Twp. 2, Rge 26 W2; NTS72H3; Zone 13, 5440250 N, 470300 E) as requested by the collector R. Sykes." Geol. Surv. Canada, Paleontology Report.

Sweet, A. R. (2007). "Applied research report on 3 samples from the Willow Bunch Lake region, Bengough (NTS 72H/6) and Minton (NTS 72H/2) map area." Geol. Surv. Canada, Paleontology Report.

Sweet, A. R., and D. R. Braman. (2001). "Creataceous-Tertiary palynofloral perturbations and extinctions within the *Aquilapollenites* Phytogeographic Province." Can. J. Earth Sci. 38: 249-269.

Sweet, A. R., and A. R. Cameron. (1991). "Palynofacies, coal petrographic facies and depositional environments: Amphitheatre Formation (Eocene to Oligocene) and Ravenscrag Formation (Maastrichthian to Paleocene), Canada." Int. J. of Coal Geol. 19: 121-144.

Sweet, A. R., and A. Chandrasekharam. (1973). "Vegatative remains of *Azolla schopfii* Dijkstra from Genesee, Alberta." Can. J. Bot. 51: 1491-1496.

Takaso, T., and P. B. Tomlinson. (1990). "Cone and ovule ontogeny in Taxodium and Glyptostrobus (Taxodiaceae-Coniferales)." Am. J. Bot. 77: 1209-1221.

Thomas, W. (chief consultant). (2003). Flora: over 20,000 plants and their cultivation requirements. Toronto, Firefly Books.

Ward, L. F. (1887). "Types of the Laramie Flora." US Geol. Surv. Bull. 37: 1-354.

Whitaker, S. H. (ed.). (1978). Coal resources of southern Saskatchewan: a model for evaluation methodology. Geol. Surv. Canada, Ec. Geol. Report 30.

Wilf, P. (1997). "When are leaves good thermometers? A new case for Leaf Margin Analysis." Palaeobiology 23: 373-390.

Wilf, P., and K. R. Johnson. (2004). "Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafloral record." Paleobiology 30: 347-368.

Willis, B. J., and A. K. Behrensmeyer. (1994). "Architecture of overbank deposits in northern Pakistan." J. of Sed. Res. B 64: 60-67.

Wing, S. L., G. J. Harrington, F. A. Smith, J. I. Bloch, D. M. Boyer, and K. H. Freeman. (2005). "Transient Floral Change and Rapid Global Warming at the Paleocene-Eocene Boundary." Science 310: 993-996.

Wing, S. L., and L. J. Hickey (1984). "The *Platycarya* perplex and the evolution of the Junglandaceae." Am. J. of Bot. 71: 388-411.

Wolfe, J. A. (1977). "Paleogene floras from the Gulf of Alaska region." US Geol. Surv. Prof. Pap. 997: 1-108.

Wolfe, J. A. (1990). "Palaeobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary." Nature 343: 153-156.

Wolfe, J. A. (1993). "A method of obtaining climatic parameters from leaf assemblages." US Geol. Surv. Bull. 2040.

Wolfe, J. A., and R. A. Spicer. (1999). Fossil Leaf Character States: Multivariate Analysis. *In* Jones, T. P. and N. P. Rowe (eds.) Fossil Plants and Spores: Modern Techniques. London, Geological Society: 233-239.

APPENDIX A

Taxonomic Re-evaluation of Paleogene *Glyptostrobus*

Introduction

Glyptostrobus Endlicher 1847 contains one extant species, *Glyptostrobus pensilis* (Stauton ex D. Don) K. Koch 1873, with a limited range in Southeast Asia. It is unclear whether this species occurs in the wild, or solely in cultivation (Farjon 2005). The present range of the species is considered warm temperate to tropical, with a preference for wet soils. Although currently geographically restricted to Southeast Asia, fossil remains identified as *Glyptostrobus* are relatively common and circumboreal. The fossil record begins in the Late Cretaceous in North America and northeast Asia, gaining a pan-boreal distribution by the Miocene, then becoming severely restricted during the Pliocene and Quaternary (LePage 2007).

The extant species, *Glyptostrobus pensilis*, exhibits a wide variety of foliage morphologies, including cupressoid, cryptomeroid and taxodioid foliage and all variations inbetween (Christophel 1976). The foliage can closely resemble that of other living genera, including *Cryptomeria* D. Don, *Taxodium* Richard, *Sequoia* Endlicher, *Sequoiadendron* Buchholz, *Metasequoia* Miki, *Juniperus* L., *Athrotaxis* D. Don, *Araucaria* Juss. and *Taxus* L., among others. As is common in conifer taxonomy, the seed cones provide a firmer foundation for characterization. The seed cones are distinctive, and described as pyriform and consisting of 20 to 22 cone scales arising from a basal disk. These scales consist of a flattened and largely fused bract scale complex (fig. A1), with bracts shorter than the scales (Takaso and Tomlinson 1990). The bract forms a reflexed structure referred to in descriptions as a mucro, which protrudes from the abaxial face. The margin of the scale consists of 7-11 lobate teeth, and on the adaxial surface of the scale are a pair of winged seeds, although few scales in each cone produce viable seed.

The taxonomy of Paleogene *Glyptostrobus* has been debated for over 100 years, since the first fossil cones were discovered in North America. Initially, these remains were placed, with some trepidation, in *Glyptostrobus europaea* (Brongniart) Unger (Berry 1916) (formerly *G. europaeus*, see Paclt 1997), a European species described from the Neogene. Brown (1936) reevaluated the North American record, and

established two species of American *Glyptostrobus*: *G. dakotensis* Brown from the Paleogene (described as the "Eocene" in the paper, as the Paleocene had yet to be differentiated); and *G. oregonensis* Brown from the Miocene. Brown (1962) later revised *G. dakotenis* to be synonymous with *Sequoia nordenskioldii* Heer, a taxon based on foliage from the Paleogene of Spitzbergen that he felt was the same as that associated with cones published as *Cryptomerites lambsii* Bell (1949), which he considered synonymous with in *Glyptostrobus dakotensis*.

In the 1970s, many authors revisited the taxonomy proposed by Brown (e.g. Butala and Cridland 1978; Hickey 1977). Each of these reports concluded that Brown's taxonomy both in initial designation and later revision was incorrect at some level. It was argued that the characters utilized by Brown were not diagnostic, and that the character states of both proposed North American species overlapped entirely with *Glyptostrobus pensilis* and *Glyptostrobus europaea*. It was proposed (Butala and Cridland 1978) that until statistics or obvious variation shows all *Glyptostrobus* should be united in a single fossil taxon, *G. europaea*, with the exception of *G. comoxensis* which they felt was not *Glyptostrobus*.

Exceptionally well preserved, mummified fossil seed cones of *Glyptostrobus*, as well as an abundance of foliage, has been recovered from Eocene of Axel Heiberg Island, Canadian High Arctic, prompting a re-evalutation of the taxonomic status of North American remains of the genus.

Materials and Methods

Materials for this study have been collected from Paleogene outcrops from northern and western Canada. Thousands of *Glyptostrobus* fossils were recovered from the Geodetic Hills fossil forest localities of the Buchanan Lake Formation (79^{o}54'N, 89^{o}20'W), on Axel Heiberg Island, Canadian Arctic Archipelago, by J.F. Basinger and associates (1984-2004) (fig. A2). The Buchanan Lake Formation is the youngest unit in the Eureka Sound Group, and consists of three member units: a lower coal member; a conglomerate-sandstone member; and an upper coal member (Rickets 1991). The majority of the material examined in this study comes from the upper coal member, from two especially rich beds designated University of Saskatchewan Paleobotanical

Collection US 190 (B`-level) and US 415 (N-level). Additionally, numerous specimens from US 231 and US 234, both within the lower coal member, were recovered and examined. The beds of the upper coal member are considered Middle to Late Eocene on the basis of structural evidence (Ricketts 1991) as well as palynology (McIntyre 1991) and the occurrence of Brontothere teeth (Eberle and Storer 1999). The lower coal member is also considered Eocene in age. The beds of the Buchanan Lake Formation consist largely of fine-grained fluvial, lacustrine and floodplain sediments deposited during uplift of the Princess Margaret Mountains during the Eurekan Orogeny (Miall 1986; Rickets 1991). There are no geochronologically dateable igneous rocks in the area to facilitate numerical dating.

The fossils include complete seed cones, seed-cone scales, seeds, foliage and pollen cones. Some specimens were cleaned by submersion in concentrated hydrofluoric acid to remove adherent sediment in order to reveal fine details. Cuticle extraction was attempted from locality US 234 specimens utilizing CrO_3 (Alvin and Boulter 1974), Bleach, and Schultze's Solution, with the latter most successful on the fossil material. The exposed cuticle was delicate and subject to fragmentation in the extraction process.

The second principal population examined in this study was recovered from the Paleocene Ravenscrag Formation exposures on the banks of the Big Muddy Valley, Willow Bunch Lake map area (72H) (fig. A3), in southern Saskatchewan. *Glyptostrobus* cones and scales were collected from numerous localities of basal Paleocene age along the valley, as well as one locality of Middle Paleocene age. Over 50 loose cone scales, 15 complete seed cones and one seed have been recovered from this area, as well as hundreds of impressions and coalified foliar segments, all lacking cuticles. These fossils were prepared by light degagement.

Additional specimens of Paleocene *Glyptostrobus* curated at the University of Alberta and University of Saskatchewan collections, representing numerous localities in the Cypress Lake map area of southwestern Saskatchewan (U of S), the Smokey Tower Formation in Northwestern Alberta (S3465, S3532)(U of A) and the Joffre Roadcut locality of southern Alberta (S40980, S40981, S41009, S41019, S41023, S41033,

S41038, S41063, S41177, S41212, as well as additional specimens that had yet to receive an ascension number in 2005) (U of A), were also examined.

Specimens classified as *Glyptostrobus europaea* Heer from Miocene localities in Turkey, held in the collections of the University of California at Berkley, were also photographed and measured to provide data from a European population (2886, 2887, 2888, 5939, 5944) . Specimens from the Miocene of Oregon, USA, representative of what Brown (1936) proposed as *G. oregonensis*, held in the Florida Museum of Natural History collection (UF 18161, UF 18240, UF 18848, UF 18850, UF 18852, UF 18853, UF 18856, UF 18860), were also examined.

Other comparisons were based upon specimens illustrated and described in the literature under various taxonomic names. Nevertheless, of the numerous traits measured as part of this study, only two are commonly recorded in the literature: seed cone width; and seed cone length. Some papers also include data on the dimensions of the seed cone scales. Where additional data could be derived, this was included within the newly assembled data set.

In addition, four reasonably complete seed cones, and approximately 100 seed cone scales along with many foliar specimens of *Glyptostrobus pensilis* K. Koch collected from the Nagoya Botanical Gardens in Japan by J.F. Basinger and E.E. McIver in 1994 were included in this study.

Numerous features of the seed cones were measured for this study: the width (a) and length (b) of the entire cone; width (c) and length (d) of fertile scales; width of the bract (e) on measured fertile scales; the number of cone scales; number of marginal teeth on the scales; the length of the shoot bearing the cone (f); and the length of the leaves on the shoot (g) (fig. A4). Not all of these features were available for all specimens.

The four most commonly available traits of the seed cones (table A2) were grouped through multivariate analysis, utilizing a copy of PC Ord version 3.20. They were grouped through Euclidean clustering using Ward's method, as this method produced the least chaining. Other methods of clustering were also tested to verify that Ward's method produced the least chaining.

Systematics

Order— Coniferales

Family— Cupressaceae Rich. ex Bartl. Sensu Eckenwalder 1976

Genus— *Glyptostrobus* Endlicher 1847

Species— *Glyptostrobus dakotensis* Brown 1936

Synonyms and References:

Glyptostrobus europaea auct. non (Brongn.) Unger, Newberry, 1898, p. 24-25, pl. XXVI, fig. 8a; Hickey, 1977, p.110-111, pl. 5 figs. 12-14, pl. 6, fig. 1; Hoffman, 1995, p. 31-32, pl. 5, figs. 35-41.

Glyptostrobus dakotensis Brown, 1936, Journ. Wash. Acad. Sci. 26: 355-356 figs. 2, 3; Pabst, 1968, p. 50-51, pl. 12, figs. 1-3.

1949: *Cryptomerites lambsii* Bell, 1949, p. 49, pl. 29, figs. 2, 4, pl. 30, figs. 1, 3-5, pl. 31, fig. 4, pl. 32, figs. 2, 4.

1962: *Glyptostrobus nordenskioldii* (Heer) Brown non *Sequoia nordenskioldii* Heer, 1962, p. 49, pl. 11, figs. 3, 7-22 (pro parte, only including the synonymies listed here); Christophel, 1976, p. 17, pl. 6, figs. 35, 37-41, pl. 7, figs. 42, 44, 45, pl. 8, fig. 42, pl. 9, figs. 52-54a, 56, pl. 10, figs. 58-60, pl. 11, fig. 64, pl. 12, fig. 68; McIver and Basinger, 1993, p. 25, pl. 11, figs. 4, 5, pl. 12, figs. 1-6.

1998: *Glyptostrobus sp.* - Aulenback and LePage

Epitype: fig. A8.

Original diagnosis (Newberry 1898, p. 24): “Branches slender, bearing many branchlets; leaves of two forms, one short, thick, and appressed, the other longer (one-half inch), slender, divergent, acute, the shorter form carinated, the lonter less distinctly, if ever so; male catkins small, terminal, globular, composed of a few shield-shaped scales; fertile cones larger, ovoid in form, scales narrow, wedge shaped at base, at summit expanded, semicircular, with waved or crenate margins, the dorsum of each more or less distinctly marked with 10 to 12 acute, radiating carinae.”

Emended diagnosis: Foliage cupressoid to taxodioid, helically arranged, commonly appearing alternate distichous; sheathing bases, quadrangular in cross section; foliage on shoots subtending the cones crypto-cupressoid; stomata in rows in grooves on both faces

of the leaves, oriented randomly with a tendency towards paralleling the leaves, usually 5 ancillary cells, monocyclic, quadrangular outline to all cells, all straight edged. Ovulate cones terminal on shoots bearing cupressoid to cryptocupressoid leaves on otherwise undifferentiated shoots, at least 5 mm long; cones globose to pyriform, 8 to 17 mm long, 6.5 to 15 mm wide; 12 to 21 ovuliferous scales per cone, helically arranged, arising from a basal disk; scales triangular to flabelliform, 5 to 15 mm long, 3 to 11 mm wide, with a rounded, acute or cordate margin, with (0-) 5-11 (-17) uneven marginal teeth; bract forms a prominent mucro on the abaxial face of the scale immediately proximal to the flaring point of the scale, 3 to 7.5 mm in width, initiating larger than the scale in forward orientation, becoming reflexed with age; cones contain fertile and infertile scales, fertile scales bear 2 seeds; seeds with one large wing attached obtusely to the basal nutlet, born upright on the adaxial surface, leading to 2 prominent scars. Pollen cones terminal on undifferentiated shoots, closely resembling foliar buds.

Description

Glyptostrobus dakotensis seed cone scales are found both articulated and separately in all of the Paleogene localities utilized in this study. Each "scale" is actually a bract-scale complex, where there is a proximal fusion of the bract and cone scale, but a distal separation. The distal margins of the scales are variable, and produce a wide variety of morphologies. Every scale, even within the same cone, has a unique morphology. The length to width ratio of the scales varies from 1:1 to 3:1, with the vast majority around 1.5:1. Marginal teeth are common features, although not all scales have marginal teeth. The teeth are unequal in size and spacing across the margin. They can be marginal or sub-marginal, conic or blade shaped (fig. A5). Some appear lobe-like (fig. A5). Each tooth on a margin may have a different size and shape. The marginal teeth may point forward or radiate from a central point. Some scales exhibit acutely or obtusely rounded margins, which can have a central point. Some specimens show a central cleft, leading to two broad lobes. The bract initially is larger than the scale and has a forward orientation. As the cones mature, the bracts become reflexed.

Seed cones of *Glyptostrobus dakotensis* are typically globose and obovate, although relatively rare pyriform cones occur as well. The length to width ratios of the

cones ranges from 1.5:1 to 0.6:1, with the vast majority at about 1:1. The cone scales originate from a basal disk. However, it is common for the central scales to resemble a central axis in seed cones of all known *Glyptostrobus* species. One aberrant specimen (University of Alberta Palaeobotanical collection S41033) has a central axis (fig. A6). This only affects the central scales, which are typically misshapen and nearly fused (fig. A7), so the fusion of these scales into a central axis is not unexpected.

Seeds occur in vertical pairs on specific scales within each cone. Seeds of the Paleogene fossil material have 2 equal wings and an ovate nutlet. At least 8 seeds are found in each cone, although it is unclear how many of these are viable.

The seed cones occur terminally on unspecialised shoots. It is common for these shoots to arise in close proximity to one another on a larger branch (fig. A8). The shoots are 5 to 20 mm long. The subtending shoot always is completely covered in cupressoid foliage.

Leafy shoots of the Paleogene fossil collections considered as *Glyptostrobus* exhibit a wide range of variation (see Christophel 1976). Shoots with cryptomeroid, cupressoid and crypto-cupressoid foliage have been found attached to ovulate cones in many localities. Leaves on these shoots are decurrent, sheathing the stem and the bases of adjacent leaves, so that accurate measurements of leaf length are difficult to determine. Specimens exhibiting crypto-taxodioid and taxodioid foliage are consistently found in beds containing diagnostic cones, and no other appropriate ovulate cones have been found associated with foliage of this morphology. However, they have yet to be found in attachment with the seed cones in these localities. All of the foliage has acute tips with quadrangular cross sections. A singular vascular trace runs through the centre of each leaf. Stomata, when visable, are located primarily in bands in the troughs of the leaves, but they are amphistomatic.

Cuticular structures present on the extracted associated leaves from USPC 234 exhibit incompletely to completely dicyclic stomata with 5 (4-6) subsidiary cells. The stomatal complexes in the fossil cuticle from Axel Heiberg are 27µm ± 3 µm long and 18µm ± 2 µm wide.

Structures interpreted to be pollen cones occur terminally on unspecialised shoots. These shoots are often in close proximity, resulting in a pseudo-panicle. In situ

pollen has not been recovered from the pollen cones of any of the localities. Therefore, some trepidation has been raised about whether these structures are merely foliar buds or are actually pollen cones, and they are not included in the diagnosis. *Glyptostrobus*-type pollen is often found in palynological studies of these beds (Sweet 1997; Sweet 2007).

Glyptostroboxylon wood has been found with the Axel Heiberg specimens. However, none of it is found attached to the shoots or cones, so it is not included in this species.

Discussion

Identifying Material as *Glyptostrobus*

The presence of scale leaves and bract-scale complexes indicates that the Paleogene fossil materials have an affinity with the Cupressaceae (*sensu* Eckenwalder 1976). The foliage and cone scales are not arranged in opposite pairs, establishing affinity with the subfamilies Sequoianae, Taxodianae, Taiwanianae, Cunninghamianae or Athrotaxinae. The bract-scale complexes are non-peltate, and have emergent bracts, which are shorter than the scales. This indicates affinity with the Taxodianae and not the other sub-families. Extant Taxodianae includes *Taxodium*, *Glyptostrobus* and *Cryptomeria* (Farjon 2005). Of these, the fossil materials do not resemble *Taxodium*, as the seed cones are borne terminally on regular shoots and the cone scales are non-peltate, both of which are used in the extant to distinguish between *Glyptostrobus* and *Taxodium*. The scale margins are also highly toothed, which is more common in *Glyptostrobus* and *Crypromeria*. Where it has been observable, the seed cone scales arise from a basal disk instead of a central axis in the fossils, which is a trait of *Glyptostrobus* and not *Taxodium* and *Cryptomeria*. Between *Cryptomeria* and *Glyptostrobus* the Paleogene fossil materials more closely resemble *Glyptostrobus* due to the rare presence of taxodioid foliage, the basal origination of the cone scales and the high irregularity in presence, number and morphology of the marginal teeth of the cone scales. All traits conform to belonging to the genus *Glyptostrobus* as it is currently circumscribed.

Characters Utilized

This study focuses on the seed cones, widely considered to include the defining characters for conifer taxa (Farjon 2005). Difficulties arise from assigning fossil foliar remains to fossil *Glyptostrobus* spp., as the defining traits of *Glyptostrobus pensilis* foliage are broad. Instead, characters of ovulate cones were examined to provide species characters, as the material can be definitively assigned to the genus. Only the dimensions of the scales and entire cones are consistently recorded in the literature; therefore, these traits were chosen for the primary comparison in this study.

Cluster analysis of the seed cone traits shows two groups, one consisting of the Paleogene material and the other encompassing the extant and the Neogene material (fig. A9). Within the Paleogene cluster, multiple groups exist. The material collected from the three populations on Axel Heiberg Island cluster with specimens collected from Ravenscrag Butte by McIver and Basinger (1993). The remainder of the Paleogene specimens cluster together as another branch of this tree. Both of these branches are close enough to be considered on species, for which the name *Glyptostrobus dakotensis* was chosen. The Paleogene specimens are united as one species as the cones are rounder with proportionally broader scales than the specimens from the Neogene and the extant. Within the Neogene cluster there is a tight clustering of most of the elements, with *Glyptostrobus rubenosawaensis* Matsumodo, Ohsawa, Nishida and Nishida as a distant outgroup of the other neogene populations. The tight cluster is made of both fossil species and *G. pensilis*. Three species are identified from the Neogene cluster: *G. pensilis*, *G. europaea* for fossils that cluster tightly with *G. pensilis* and *G. rubenosawaensis*. Justification of why these names were chosen is found in the next section.

Besides seed cone sizes, other traits were considered, including teeth per scale, dimensions of the bract after exertion, subtending branch dimensions, dimensions of the foliage on the subtending branches, the number of cone scales, cone shape and the ratios between these traits. However, these traits are not quantifiable on many specimens so were not included in the clustering. However, these traits illustrate further differences between the four recognized species. Table A1 summarizes the character traits for the

four recognized *Glyptostrobus* species: *G. pensilis*, *G. europaea*, *G. dakotensis* and *G. rubenosawaensis*.

Glyptostrobus Taxonomy

Cluster analysis indicates the need for the utilization of four species for *Glyptostrobus*. One of these species is the extant species, *Glyptostrobus pensilis*. The other three are fossil species. The taxonomy of fossil *Glyptostrobus* is complex, with numerous species being applied to every portion of the plant. A recent list of many of these species was recently compiled (LePage 2007). From this list, the three fossil species were identified that reflect the findings of the cluster analysis (fig. A9). The fossil species were found to be *G. dakotensis*, *G. europaea* and *G. rubenosawaensis*. The justification as to why these species were chosen is discussed below, under the heading of each of these species.

In conducting the determination of what the three fossil species should be, this study recognized that *G. nordenskioldii* (Heer) Brown, *G. oregonensis* Brown, *G. comoxensis* Bell, *G. dunoyeri* (Gardner) Boulter and Kvacek and *G. orientalis* Endo also deserve comment. Each of these additional species receives commentary under its own heading below, much like the three accepted species have.

Glyptostrobus dakotensis Brown

In the initial description of *Glyptostrobus dakotensis* Brown, three primary differences were recognized between *Glyptostrobus europaea* and the Paleogene material of North America (Brown 1936). First, the seed cone scales were shorter and broader in *G. dakotensis* than in *G. europaea*. Second, cone scales are found isolated more often in *G. dakotensis* than in *G. europaea*. Third, *G. dakotensis* is found in the Paleogene. These three traits are not stated quantitatively, and therefore were rejected by Butala and Cridland (1978) as being undiagnostic. Based on the type material, this rejection seems justified, as Brown (1936) developed the species from only three specimens, not a diagnostic representation. However, more extensive collections were subsequently recovered from many localities throughout the North America. These collections support the first two criteria of his initial diagnosis. Measurements

conducted as part of the present study indicate that the first character, that the cone scales are, in general, shorter and broader is accurate. The length to width ratios of the cone scales averages 1.5 in the Paleogene material and 2.5 both *G. pensilis* and *G. europaea*.

The second character, the fragility leading to the degree of disintegration of the cones, where Brown recognized isolated cone scales as more common than in other deposits, is more difficult to quantify. Many isolated scales are found in the Paleogene material. Scales outnumber complete cones in all of the study sites. However, it is unclear the exact proportions of this outnumbering, whether the majority of cones disintegrate or not. Determining this proportion is complicated by collector's bias towards collecting complete cones over loose scales. Cone scales are often overlooked or left as undesirable specimens. Additionally, they are often not examined and recorded, even when collected. The Axel Heiberg specimens, which are projected to be typical of all Paleogene specimens show a fragile connection between the scales and the originating disk, resulting in semi-deciduous to deciduous scales that are lost at maturity. However, extant cones appear to also show a loss of scales. Unfortunately, this trait has not been extensively documented in extant populations, so it is unclear how common it is, and whether it is comparable to the Paleogene material. Additionally, loose cone scale data have not been published for *G. europaea* populations. Again, this may reflect a sampling and reporting bias, as loose scales are often observed but rarely documented (Z. Kvacek, personal commication 2006).

The third trait, an age gap of up to 30 million years, is a poor diagnostic character for specific diagnosis as it is not a morphologic trait. Significantly, there are conifer genera and possibly species that appear to have existed relatively unchanged for up to 100 million years. Some fossil conifers from the Cretaceous are even indistinguishable from the extant to the specific level, such as *Taiwania cryptomerioides* Hayata (D. Lindsay, personal communication 1999). Therefore, specimen age should not be used as a taxonomic designator, although interesting for evolutionary discussion. If there are morphological arguments for splitting species, age differences can support these distinctions, and lead to a more satisfactory division.

Glyptostrobus dakotensis was chosen as the basionym for this species, contrary to Brown's later synonymization of this taxon into *G. nordenskioldii* (Brown 1962). The current study believes that *Sequoia nordenskioldii* is too ambiguous to include in synonymy with *G. dakotensis*. The current study feels that many of the specimens included in the intial synonymy list of *G. nordenskioldii* presented by Brown (1962) are not *Glyptostrobus*, but instead are other taxa like *Sequoia* as they were initially designated. Therefore, the synonymies identified by Brown (1962) have been reduced to only those that have full confidence of identification due to the presence of seed cones. Additionally, many specimens included in *G. dakotensis* in the current study were also published under the name *G. nordenskioldii*. Further discussion on the status of *G. nordenskioldii* is found below.

***Glyptostrobus europaea* (Brongniart) Unger**

Glyptostrobus europaea was the first named fossil species for *Glyptostrobus*. In standard practice, it is considered nearly identical in morphology to *G. pensilis*, but is not synonymized with *G. pensilis* as it is a fossil, so it should not be assumed that it is identical in all characters to *G. pensilis* (Hickey 1977; Butala and Cridland 1978). This study agrees with this interpretation; however, it finds that there are numerous slight differences between *G. pensilis* and *G. europaea*, which can be seen in table A1. This supports not synonymizing *G. europaea* and *G. pensilis*, despite clustering as indistinguishable from one another, as variation shows that they were not identical. *G. europaea* expresses more variability in most of the observed traits (table A1). However, given that *G. pensilis* only exists in limited stands where it has begun to suffer diversity loss, this decreased variation in *G. pensilis* is expected.

Due to the use of *Glyptostrobus europaea* as the default, many of the specimens that are now included in *G. dakotensis* were classified initially as *G. europaea*, including the types identified (Brown 1936) and many specimens published since the proposed rejection of *G. dakotensis* and *G. nordenskioldii* by Hickey (1977), and Butala and Cridland (1978). To facilitate clarity after the unification of species in this study, specimens that are included in the synonymy of *G. dakotensis* are not reffered to as *G. europaea*, but instead are referred to by the locality they were found at. This eliminates

the potential confusion that would be caused by seeing *G. europaea* in the *G. dakotensis* cluster. The specimens called *G. europaea* include specimens from the Miocene of Europe and Turkey, which are close to the types.

***Glyptostrobus. rubenosawaensis* Matsumodo, Ohsawa, Nishida and Nishida**

Glyptostrobus rubenosawaensis is a species known from one Miocene locality in Japan (Matsumodo et al. 1997). This species was diagnosed as new due to larger cone sizes and more prominent bracts compared to all other *Glyptostrobus* species. 22 specimens were recovered to from the type locality, which is the only population known of this species.

In the recognition of *Glyptostrobus rubenosawaensis*, Matsumodo et al. (1997) consider seed cone size, bract-scale complex size, and emergant bract size to be important characters for designating new species of fossil *Glyptostrobus*. The clustering of these measurements conducted in this study places this material more closely to *G. pensilis* and *G. europaea* (fig. A9). However, it is distanced from the other members of this cluster, and, therefore, this species stands as a separate entity from *G. europaea*.

In the proposed rejection of the North American fossil *Glyptostrobus* species by Butala and Cridland (1978), they suggest that new species of *Glyptostrobus* should not be established unless there are obvious differences, ideally backed up with statistics. *Glyptostrobus rubenosawaensis* meets these criteria. The characters used to initially distinguish *G. rubenosawaensis* from *G. europaea*, which include seed cone size and size of the emergant mucronate bract, are the same ones used by this study to distinguish *G. dakotensis* from the other *Glyptostrobus* species. That *G. rubenosawaensis* clusters more closely to *G. europaea* utilizing these traits, yet is still considered a separate and valid species supports the resurection of *G. dakotensis* as a valid species, which clusters more distantly from *G. europaea*.

***Glyptostrobus nordenskioldii* (Heer) Brown**

In 1962, Brown synonymized many taxa into his concept of a Paleogene *Glyptostrobus* species. The foliar species *Sequoia nordenskioldii* Heer was chosen by Brown (1962) as the basionym due to priority. As mentioned above, the distinguishing

characters for conifer species are spread throughout the plant, with a particular emphasis on the female reproductive structures. This is especially true with *Glyptostrobus*, where the foliar traits are diverse. Unfortunately, *Glyptostrobus* cones have not been recovered from the type locality of *Sequoia nordenskioldii* on Spitzbergen Island (Schwietzer 1974). However, other features of the foliage show that this material likely is *Glyptostrobus*, and given that the age is Paleogene, it may be reasonable to assign the material to the same species as the North American and Asian Paleogene *Glyptostrobus* populations. However, it seems best to reject Brown's decision to use *S. nordenskioldii* as the basionym, due to the absence of cones in the type material. As such, it is somewhat unclear what taxon this material represents. It is safest to consider this foliar material *"Sequoia" nordenskioldii* Heer with a note that this material resembles *Glyptostrobus* more closely than the other extant genera, due to its heteromorphic foliage. It is not included in the current synonymy.

***Glyptostrobus oregonensis* Brown**

Glyptostrobus oregonensis was erected for *Glyptostrobus* specimens from the Neogene of North America by Brown (1936), during which time the distribution of the genus had started to become limited. Brown differentiated this species from *Glyptostrobus europaea* based on two criteria: 1. Cones are longer and narrower, more pyriform; and

2. The edges of the cone scales are less crenulated, almost smooth.

Specimens of this species have been recovered from western North America throughout the Miocene. No specimens have been discovered in Pliocene beds in North America, and it seems that *Glyptostrobus* had been extirpated from North America prior to the Pliestocene. Specimens that exhibit seed cones, stored in the Florida Museum of Natural History (UF 18161, UF 18240, UF 18848, UF 18850, UF 18852, UF 18853, UF 18856, UF 18860), were measured for comparison in this study. Cluster analysis places these cones within the ranges of extant *Glyptostrobus pensilis* along with *G. europaea* (fig. A9). As can be seen in the clustering, both *G. oregonensis* and *G. europaea* cluster with *G. pensilis*, making it impossible to satisfactorily distinguish these taxa from one another besides the division between fossil and living. *G. oregonensis* is considered a

junior synonym of *G. europaea*, as the morphological differences are not great enough to distinguish the two populations.

***Glyptostrobus comoxensis* Bell**

Glyptostrobus comoxensis was named from Late Cretaceous specimens of the Nanaimo Group of British Columbia by Bell (1957), who distinguished these specimens from other *Glyptostrobus* species by the smooth margins of the cone scales. Unfortunately, these specimens are poorly preserved and classification is aggravated by Bell's painted outlines on the specimens used to illustrate his proposed characters. Specimens of *Glyptostrobus* populations occasionally exhibit smooth margins. In particular, *G. dakotensis* exhibits both smooth and dentate margined specimens, often in the same cone. Of more concern, a lack of lobes in the cone scales and nearly apical emergence of the bracts, challenges the placement of this material into the genus *Glyptostrobus*. Instead, it likely belongs to an extinct sister taxon (Boyd 1992, Aulenback and LePage 1998). However, reclassification of these remains is beyond the scope of this paper.

***Glyptostrobus dunoyeri* (Baily) Boulter and Kvacek**

Glyptostrobus dunoyeri (Baily) Boulter and Kvacek was established for specimens collected from European Paleogene localities including Ballypalady, Mull, Spitzbergen and eastern Greenland (Boulter and Kvacek 1989). The basionym of this species was *Sequoia dunoyeri* Baily, a foliage species from Ballypalady. However, the cones of *Cryptomeria sternbergii* (Goeppert) Gardner were included in the synonomy list. These cones are poorly preserved, so this species is primarily considered through its foliage. In particular, the cuticular features are the most important characters for this species, which Boulter and Kvacek feel most closely resemble *Glyptostrobus europaea* (Brongniart) Unger. Details of the cones are not considered in depth. However, the diagnosis lists them as being 3cm in diameter and almost spherical in shape. This size and shape is unknown for other *Glyptostrobus* species. Observing the illustrated specimens, it becomes clear that the specimen that the diagnosis is derived from is Pl. 8 fig. 1 (Boulter and Kvacek 1989). This figure illustrates a large globose cone

approximately 3 cm in diameter, which does not closely resemble *Glyptostrobus* remains, but may be a species of *Cryptomeria*, as Gardner (1883) suggested. However, Boulter and Kvacek (1989) also illustrated seed cones in Pl. 8 figs. 8 and 9. These cones fit the dimensions found in the current study. However, the diagnosis does not reflect these cones. Therefore, these specimens should not be included in *Glyptostrobus dunoyeri* as presented.

There is no comparison to the North American Paleogene specimens in Boulter and Kvacek (1989), other than a shared synonomy of the *Sequoia norndenskioldii* type manterials by both *Glyptostrobus dunoyeri* and *Glyptostrobus noredenskioldi*.

It is the opinion of the current workers that as diagnosed and circumscribed, *Glyptostrobus dunoyeri* is not an appropriate name for the specimens described from the Canadian Arctic and the Western Interior of North America. It seems that multiple species are included within *G. dunoyeri* as presented, and that the specimens designated as the types are the portions of this species that represent other taxa.

***Glyptostrobus orientalis* Endo**

This species is designated on a single cone found in sediments dated from the Miocene of Korea. No illustrations were present with the initial description. Dimensions of the cone cluster with the Paleogene material from North America and not with the other Eurasian specimens. The cone is round, with scales that are broad according to the description of Endo. However, without seeing this cone, it is impossible to compare it to the North American Paleogene material. The proper identification of this specimen shall not be resolved in this paper, as the parameters of the population are unclear, as to whether this population represents a few outlier specimens to *Glyptostrobus europaea*, or whether these specimens should be a relic population of *G. dakotensis*.

Maturity

The cones of *Glyptostrobus pensilis* go through extensive changes throughout development (Takaso and Tomlison 1991). Of particular note, the diagnostic pyriform shape arises only near maturation. Immature cones are globose to obovate in

morphology, similar to Paleogene fossils. Additionally, cone scale expansion occurs largely after bract development to a large extent, so immature cones have relatively larger bracts and smaller cone scales. These resemble the traits described here for some specimens of *G. dakotensis*. Immaturity may account for some of the observed variation present in *G. dakotensis*, although it does not seem adequate to account for all variance in the characteristics. Individual cone scales are commonly found conforming to the general morphometrics of the globose cones, indicating that the scales were relatively small when the cones became brittle and subsequently disintegrated, likely for seed dispersion. Cones at all stages of maturity, including many with partial opened scales, were considered as elements in this study. Even the pyriform cones, indicative of maturity by Takaso and Tomlinson (1990) conformed to the smaller size and broader cone scales in *G. dakotensis*. Larger obovate and globose cones are part of *G. dakotensis*, exhibiting more globose and obovate cones, with broad cone scales. The clearest indicator of cone maturation is evidenced by the bracts. While still immature, the bracts will run parallel to the scales. However, when maturity is reached, the bracts become reflexed. The cones and cone scales measured for this project exhibit these reflexed bracts, no matter how large the cones were. Therefore, although the morphology seems more juvenile, they also exhibit mature traits. For example, mature cone scales are more likely to be found loose in the sediment, as mature cones are prone to disintegration.

Conclusions

Four species of *Glyptostrobus* are recognized by this work, dertermined initially clustering and tradition, but supported by numerous characters (table A1). Most of these characters are related to characters of the seed cones. Foliar and pollen cone gross anatomy is similar for all four *Glyptostrobus* species. Foliage is recognized as exhibiting numerous morphologies, ranging from cupressoid to taxodioid with all intermediates occurring, and can be easily confused for not only other species of *Glyptostrobus* but also other conifer genera (Christophel 1976; Farjon 2005). However, *G. dakotensis* exhibits differences compared to other *Glyptostrobus* species in foliar cuticular traits, as *G. dakotensis* has stomatal complexes approximately half the size of

the stomatal complexes described in both *G. pensilis* as well as *G. europaea*. However, *G. dakotensis* cuticle is rarely found. A summary of the different traits is found in Table A1.

The synonymies of *G. dakotensis* have been kept tight, to eliminate the confusion that has been present in the taxonomy of the species. Only collections with seed cones and/or seed cone scales have been included. It is advised that future studies wishing to include specimens in *G. dakotensis* follow this practice to avoid confusion.

An axis with multiple cone scales found at locality B` (US191) was chosen as the epitype for *Glyptostrobus dakotensis*. This specimen, which preserves multiple cones, illustrates the differences in cone morphology compared to the other *Glyptostrobus* species. This eliminates concerns of ambiguity stemming from the initial type materials of *G. dakotensis*, which are ambiguous.

Character	*G. pensilis*	*G. dakotensis*	*G. europaea*	*G. rubenosawaensis*
Seed cone shape	P, O	P , O, G	P, O	P
Seed cone length	14-25	8-17	16-24	26.2
Seed cone width	8-18	6-20	7-20	18.8
Seed cone length : width	1.6 (1.2-1.9)	1.1 (0.7-1.4)	1.4 (1.3-2.5)	1.4
Scale length	9-17	5- 16	8-17	17-23
Scale width	3-6	3-11	3-7	3.5-8
Scale length : width	2.6 (2.0-4.0)	1.5 (1.0-2.5)	2.3 (1.6-4.25)	2.8
Mucro length	0.5	1-2	1	2
Mucro width	2-4	3-7.5	2-4	?
Teeth	7-9, consistent	5-17, inconsistent	7-12, consistent	?
# of scales	20-22 (26)	12-21	?	15
Seed traits	Swollen ovoid body, 2 uneven wings	Swollen ovoid body, 2 even wings	Swollen ovoid body	?
Pollen cones	Terminal on unspecialized shoots	Terminal on unspecialized shoots	Terminal on unspecialized shoots	Terminal on unspecialized shoots
Foliage shape	Cu, Cr, T, all variations	Cu, Cr, T, all variations	Cu, Cr, T, all variations	C-T, all variations
Foliage length	Cu = 1-2 mm scale like, T = 6-10 mm	Cu = 1-2 mm scale like, T = 6-10 mm	Cu = 1-2 mm scale like, T = 6-10 mm	Cu = 1-2 mm scale like, T = 6-10 mm
Cuticle traits	Amphistomatic, Stomata parallel to Sub-parallel to leaf axis, (4-)5-6(-7) subsidiary cells, Incompletely to completely Dicyclic, 46 µm l, 24 µm w	Amphistomatic, Stomata random orientation, 5 subsidiary cells, Incompletely to completely Dicyclic, 27±3 µm l, 18±2 µm w	Amphistomatic, Stomata parallel to Sub-parallel to leaf axis, (4-)5-6(-7) subsidiary cells, Incompletely to completely Dicyclic, 46 µm l, 24 µm w	?
Age Range	Extant	Paleogene	Neogene	Miocene
Distribution	SE Asia (SE China, Vietnam)	North America, Asia, Europe?	North America, Europe, Asia	Japan

Table A1: Comparison of *Glyptostrobus* species. P = Pyriform, O = Obovate, G = Globose, Cu = Cupressoid, Cr = Cryptomeroid, T = Taxodioid

	Cone W (avg)	(Max)	(Min)	Cone L (avg)	(Max)	(Min)	Scale W (avg)	(Max)	(Min)	Scale L (avg)	(Max)	(Min)
US 190	10	15	7	11	14	9	5	6	4	7.5	9	6
US 415	9	11	6.5	10	11	8	4.5	5.5	4	8	10.5	6
US 231-235	9	10	8	10	12	8	5	6.5	4.5	8	10.5	6
Big Muddy	11	14	7.5	11.5	15	8.5	6	11	3	9	15	5
G. nordenskioldii Christophel 1976	12	13	10.9	15.5	17	14	5	7	4	7.5	10	5.5
G. nordenskioldii McIver and Basinger 1993	8.5	9	8	12	15	11	6	7	6	8	11	6
G. pensilis	12.75	17.5	8	19.7	25	15	4.9	6.2	4.0	12.2	16.5	9
G. oregonensis	11.9	14.5	7	19.6	23	16	4.8	7	3.5	11.6	14	9
G. sp. Joffre Bridge	13.75	17	9	13.2	17	11	6.7	9	5	10	12	7
Cryptomerites lambsii	11	13.75	8.25	12	15	9	6	11	3	9	15	5
G.europaea (Turkey)	14.5	17.5	10	19	21.5	16.5	5	6.5	4	12.5	15	10
G. rubenosawaensis	18.8	24	13	26.2	32	21	7	8	3.5	20.1	23	17
G. pensilis FOC	12	15	9	19.5	25	14	4.25	5.5	3	11.5	13	10
G.europaea	13	19	10	19	24	17	4.5	5	4	10.25	17	8

Table A2: Seed cone characters used for clustering. Characters are seed cone width, seed cone length, seed cone scale width, and seed cone scale length. 3 measurements were included for each of the populations: the average size of the population, as well as the minimum and maximum measurements taken in the population for that character.

Figure A1. *Glyptostrobus pensilis* and *Glyptostrobus dakotensis* (US190-9111) cone scales Scale bar=1cm.

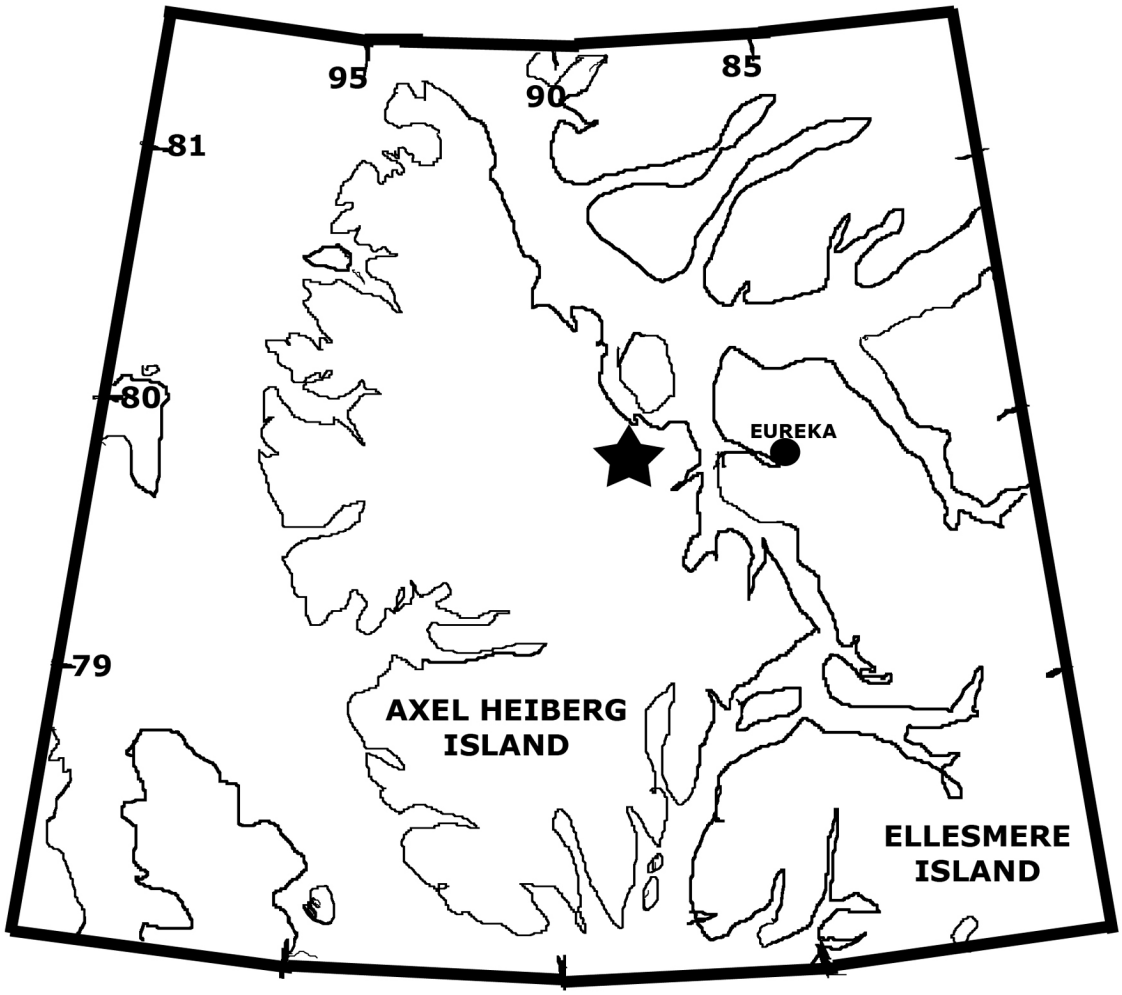


Figure A2 . Map of Axel Heiberg Island, Nunavut, Canada Star shows the localtion of the Eocene aged Buchanan Lake Fossil Forests.

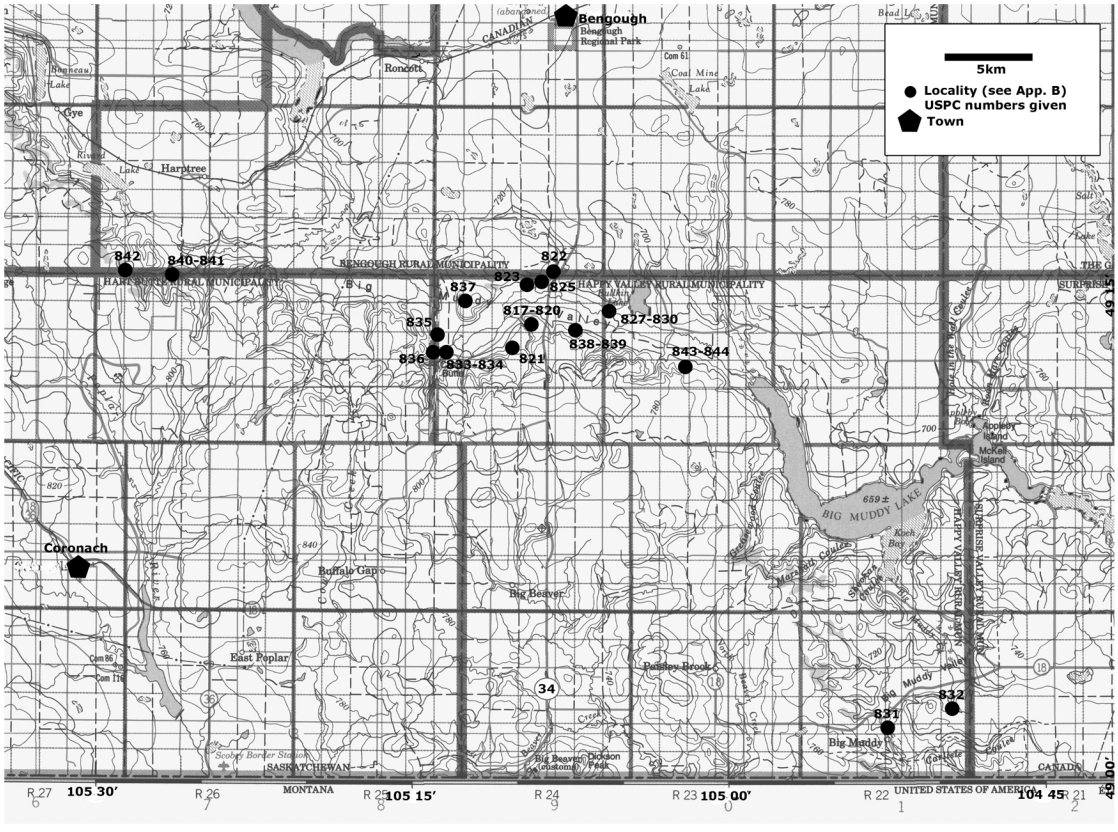


Figure 3: Map of Big Muddy Valley, Saskatchewan

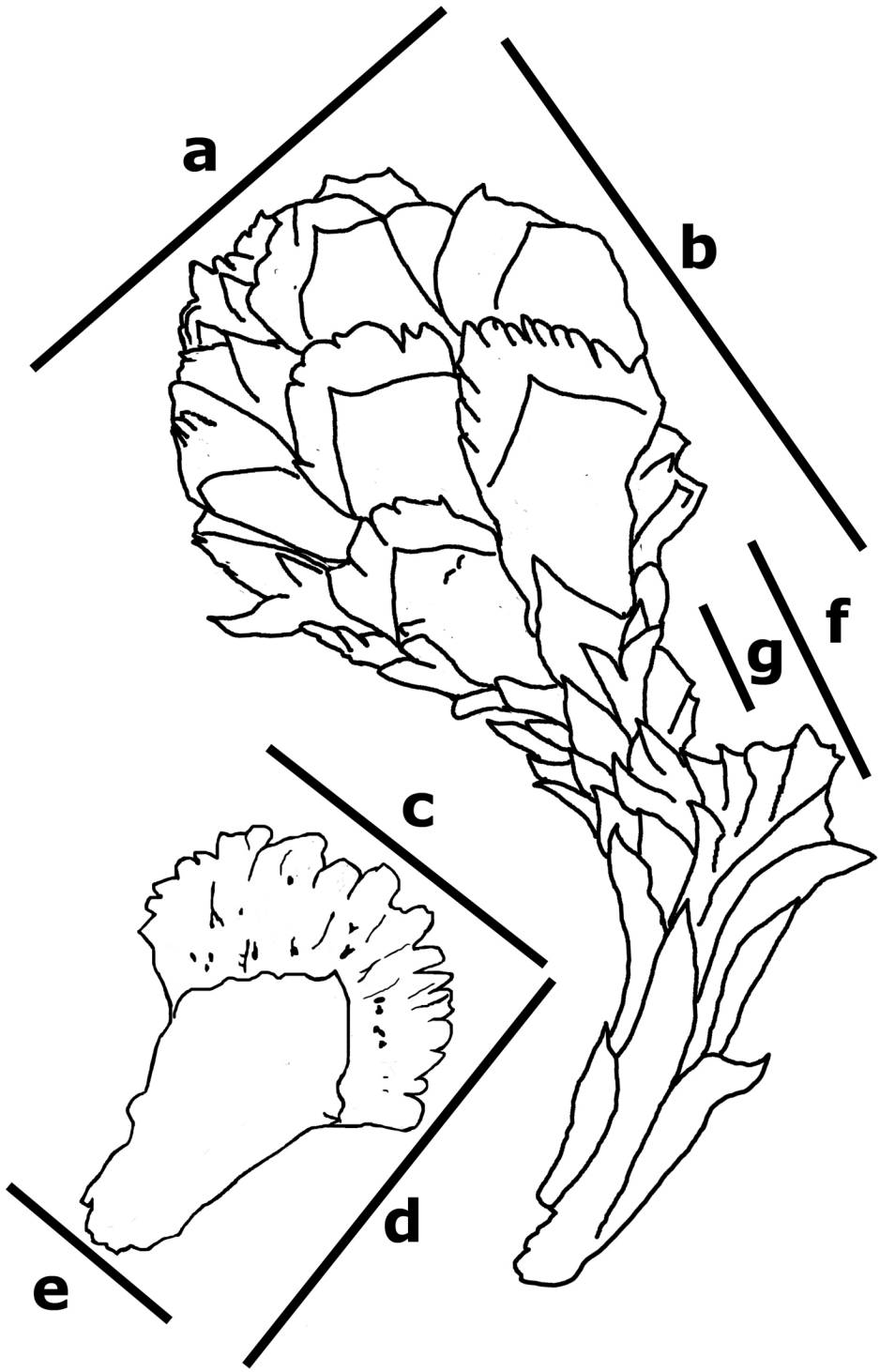


Figure A4. Cones showing dimensions measured. s is seed cone width, b is seed cone length, c is cone scale width, d is cone scale length, e is bract width, f is subtending shoot length, g is leaf length..

Figure A5. Variations of cone scales of *Glyptostrobus dakotensis*. The teeth exhibit a wide variety of morphologies. Specimens from Axel Heiberg Island. (US190-9112, US190-9113, US190-9114, US190-9111, US190-9115). Scale bar=1cm.

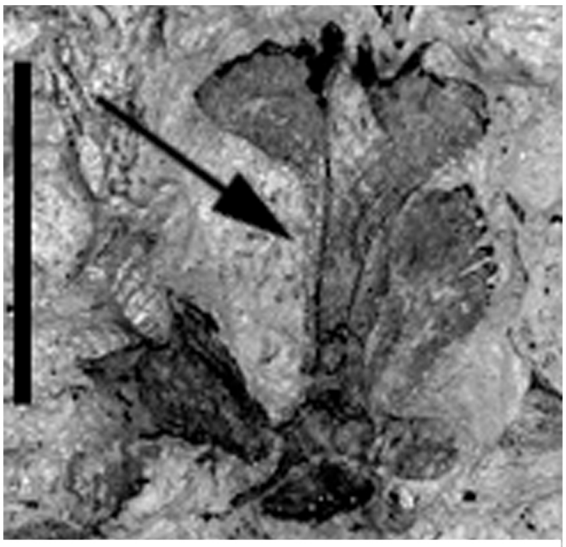


Figure A6. Aberrant central cone scale of *Glyptostrobus dakotensis*. Specimen from Joffre Bridge Roadcut locality collections of the University of Alberta (S41033). Scale bar=1cm.

Figure A7. Normal central cone scales of *G. pensilis* and *G. dakotensis* (US190-9116.) Scale bar = 1cm.

Figure A8. *Glyptostrobus dakotensis* Epitype from Axel Heiberg Island (US190-9117). Previously illustrated in Basinger (1991), McIver and Basinger (1999). Scale bar=1cm.

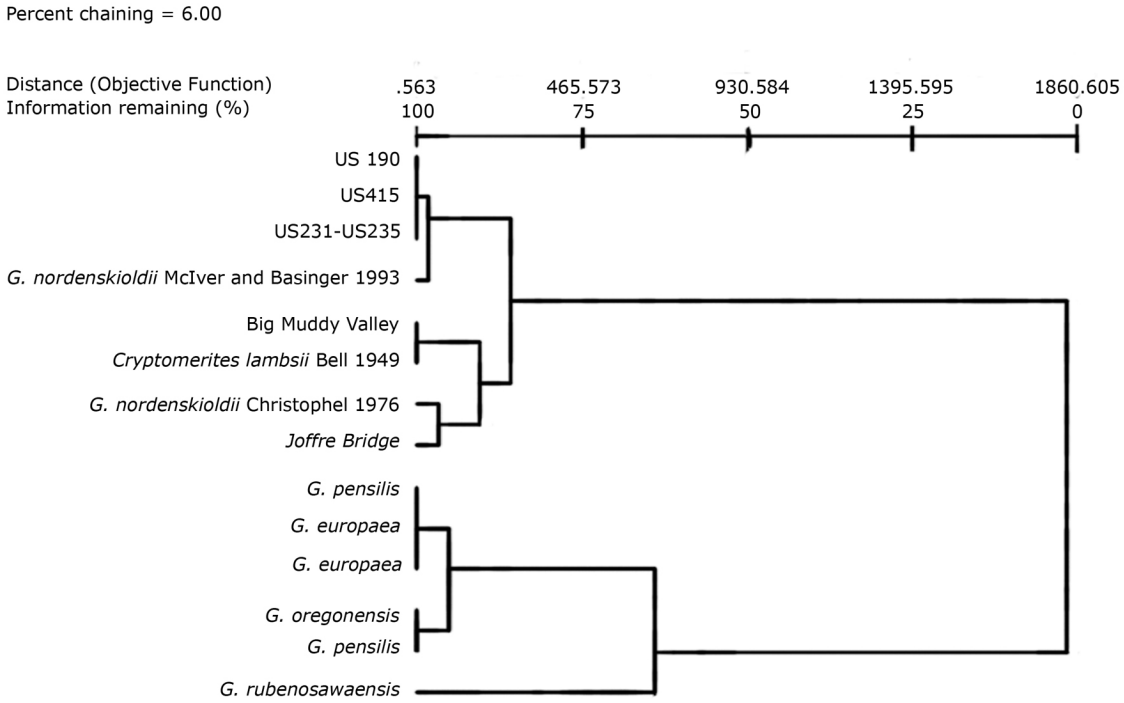


Figure A9. Clustering of *Glyptostrobus* species Using Ward's Method, Species listed in the text and in *Glyptostrobus* table 2. B' is locality US 190, N is locality US 415, 231-235 are localities US 231, US 232, US 233, US 234 and US 235, The two listings for *G. pensilis* are from the dimensions presented in the Flora of China and new materials measured for this study. *G. europaea* from the literature and from specimens stored at UC Berkley. *G. oregonensis* are from specimens from the Florida Museum of Natural History.

APPENDIX B

Collections and Access to Localities

The figured specimens are stored at the Royal Saskatchewan Museum (RSM). In addition to the collections stored at the RSM, there is at this time a large collection held by Mr. A. Larson in Bengough, consisting of thousands of specimens collected by Mr. Larson. These have been observed, and part of the collection of the RSM was gathered from them. However, specimens were left in the care of Mr. Larson either because representative specimens had already been gathered or because additional transport of the specimens would jeopardize the fossils due to the fragile nature of the specimens. Mr. Larson hopes to open a local museum, at which point the specimens would become more accessible.

Collecting in the Region

Localities US 831 and US 832 are on public grazing land, although they are managed by local farmers. All other localities are privately held, either by local ranchers or by Luscar (the owners of the Poplar River coalmine). Permission needs to be obtained to survey the area. Most of the ranchers are wary of scientific projects on their land, as unrelated projects studying the local fauna caused a disturbance, purported to lead to the dispersal and migration of the fauna from the area. There is an underlying fear and weariness amongst the local population that scientific projects will damage the area due to poor planning. Caution needs to be exercised when approaching the landowners, especially the owners of the land that houses US 845 and US 843.

If permission to collect is obtained, the ranchers will commonly request that you enter on foot, which will limit potential collecting range and quantity, as the specimens will need to be carried out. Mr. Larson has been instrumental in arranging permission for this project. However, it is unclear what future collectors will encounter in the area. There are 4 townships that need to be accounted for in this project. Maps of local land usage are currently available for the areas at the Regional Municipality offices in Bengough, Big Beaver and Coronach at the time of this thesis, although given the nature of these towns it is unclear as to how long they will remain, or continue to provide these

maps. The 4th township map is likely available in Minton, although it was not acquired for this project due to its distance from the localities.

Localities

Region 1

Region 1 refers to all localities found west of highway 34, east of Castle Butte. 5 localities were designated in this study. Localities US 817, US 818, US 819 and US 820 all occur in a coulee that runs south along the western edge of the Rhode Property. US 821 occurs to the west along the south valley wall.

US 817: 1A, Gopher Hole

N 49° 14.006, W 105° 09.680

Extensive collections were made over the years, many specimens stored in Bengough, RSM. Near to US92-4.

This site consists of a 10m long exposure about 5m tall. Numerous indistinct layers of leaf litter found starting at a layer of white clay with no remaining carbon. Name comes from Mr. Larson, who initially noted ground squirrels living in the sediments around this locality.

US 818: 1B, Easy Chair

N 49° 14.181, W 105° 09.520

Limited collections, all specimens stored in Bengough. Exposure occurs in a 1.5m runoff channel. The name is from the thought that one could set up an easy chair in the channel and collect.

US 819: 1C, Gate Site

N 49° 14.222, W 105° 09.768

Limited collections of plant fossils. A section of this exposure was taken (section US 819). Named as it occurs close to the gate of the main road, and is the only one US 817, US 818, US 819 and US 820 observable from the road.

US 820: 1D, TP site

N 49° 14.112 W 105° 09.583

Extensive collections, both in Bengough and at the RSM. Locality consists of paper shales. Found on the north side of a small hill, north of US 817, south of US 818.

Named for the need to often wrap the fossils in toilet paper to ensure safety of transport, as the shales are rather delicate.

US 821: 1E

N 49° 13.531 W 105° 10.615

Limited collections, primarily stored in the RSM. Productive plant layers found throughout. In particular, collections occurred at the base, in paper shales 6 m up and in a 7cm thick ironstone layer 13.5 m up. A section was also taken of this exposure (section US 821). Currently owned by the Holbrooks.

Region 2

Exposures along the north wall of the valley, west of Higway 34. The full extent of the region is not determined, although it is before the large point where the valley turns north, which is designated US 837. Sites collected so far only go approximately one third of the distance between Highway 34 and US 837.

US 822: 2A, Eagles Nest

N 49° 15.704 W 105° 08.483

The locality nearest Highway 34, has many productive beds including a rich *Nelumbago* bed. Eagles commonly nest on the valley walls near this locality, so caution should be exercised in collecting to not disturb them. Otherwise accessibility is high, as is diversity. Currently owned by the Holbrooks.

US 823: 2B, Dino Footprint

N 49° 15.588 W 105° 09.143

Named for structures in the Whitemud materials at the base of the cliff, which Mr. Larson thought may be dinosaur footprints. Localities many meters up the cliff wall, in a distinct overhang. Currently owned by Rhode Ranch. Diversity seems good, but is distant enough from roads to not have a full collection.

US 824: 2C, Stump Site

Furthest site west of area 2, within a lateral valley, on the east slope. Crushed petrified stumps are eroding out of the valley wall about 6 m from the valley floor. Good examples of channels slightly to the east of this locality, worth considering in sedimentological studies. On land owned by the Rhode Ranch.

US 825: 2D

N 49° 15.359 W 105° 09.032

This locality is primarily for a section. On land owned by Rhode Ranch.

US 826: 2E, Dino Footprint Upper

Near to the Dino Footprint locality, but in one of the nearby tributary valleys, slightly higher in section. On land owned by Rhode Ranch.

Region 3

North side of the valley, east of Highway 34. All on land currently owned by the Hesjdahls.

US 827: 3A, Bull Snake Site

N 49° 14.593 W 105° 05.939

Furthest west of the region 3 localities, produces leaves in dark ironstone *in situ*, specimens appearing to be purely angiosperms. No specimens collected. Named for a snake encountered when the locality was scouted.

US 828: 3B, Skinny Leaf Site

N 49° 14.455 W 105° 05.961

Unsure of original level, this locality consists of large blocks that have weathered out of the cliff and rolled down the hill. Visible slumping nearby. Named for the presence of the *Elatocladus megasequoiae*, a notable fossil.

US 829: 3C, Hesjdahl's Eagle Nest

Higher in section than where the US 828 specimens were collected. This locality has a softer matrix than the other localities in region 3, reminiscent of other regions of this collecting space, particularly locality US 822. Named by Mr. Larson for the quality of sediment, which is similar to Eagle's Nest in his opinion.

US 830: 3D, Upper Hesjdahl's

N 49° 14.903 W 105° 05.723

Higher in section than US 829. Heavy cementation, more complex root structures than other localities. Not the origin of US 828, as the flora is different. Named because it is found at the top of the hill that makes up area 3.

Region 4

Sites found on the branch of the valley running due south of Big Muddy Lake

US 831: 4A, RCMP

N 49° 01.713 W 104° 52.570

The hill to the south of the RCMP memorial (RCMP memorial is marked with a plaque). Large sandstone nodules roll down this mostly overgrown hill, particularly the south face. Unclear who owns the land.

US 832: 4B, Buff Facies

N 49° 02.172 W 104° 49.138

Due east of US 831, across a valley, hundreds of m away, but the sites are visible from them, a cream coloured bed above grey siltstones. Often forms a shelf. Currently on land owned by the province, but leased to various local ranchers. Named as it is a buff clay found above grey clays, so was initially thought to represent the buff facies of the Ravenscrag Formation. Palynology shows that it may be in fact younger than the buff facies (Sweet 2007).

US 845: 4C, Shot At site

To the north of US 832 and US 831. Permission needed as the owner is suspicious. On land owned by the Andersons. Named for Mr. Larson being shot at by a rancher when collecting.

Region 5

This region covers localities west of Castle Butte still within the valley northwest of Big Muddy Lake. This area of the valley largely runs north-south instead of east-west. This is all on land currently owned by the Paradis.

US 833: 5A, Lower Paradis

N 49° 13.110 W 105° 13.994

This site is from the base of the isolated Butte to the north of the Paradis farmstead, just to the West of where the standard grid ends. Primarily refers to the bone bed near the base of the hill. Exposure on the north face. Named as it is on a hill closest to the Paradis house on their land, and below US 834 in section. There was a bone bed in 2003 slightly below this bed, producing fragmentary remains of turtles, suchids and gar. A limited collection of these remains was taken, and are mentioned earlier in this report.

US 834: 5B, Upper Paradis

N 49° 13.013 W 105° 13.051

About 10 m up the butte from US 833. Exposure on the north Face. Named as it is on a hill closest to the Paradis house on their land, and above US 833 in section.

US 835: 5C, Too Hot site

N 49° 13.785 W 105° 14.288

About 1 km north of US 833, on the West valley wall. Visible as a prominence on the valley wall from the sites to the south. Named as the day that it was explored was hot, and this was the maximum distance willing to be traveled by all involved in the exploration.

US 836: 5D

N 49° 13.343 W 105° 14.363

Due West of US 834 on the valley wall.

US 837: 5E, Big Point

N 49° 14.921 W 105° 12.942

The corner of the north/east Valley wall. Named as it is a prominence on the north valley wall visible from the south that appears larger than all of the surrounding area.

Region 6

This region consists of the area on the south of the valley east of Highway 34 managed by the Rhode Ranch. These localities are named for Ivan Clevland, the manager of the Rhode Ranch, as he is the one who alerted us to their presence.

US 838: 6A, Ivan's Site Section

N 49° 14.383 W 105° 07.855

US 839: 6B, Ivan's Site

N 49° 14.383 W 105° 07.855

Region 7

This region is a number of exposures in coulees west of the valley, north of the Poplar River Mine. The localities are named for the rancher that manages them, Mr. Foley.

US 840: 7A, Foley's

N 49° 15.845 W 105° 27.556

A white clay layer expressed through the area. Has a unique floral composition.

US 841: 7B, Fullie's

Specimens from a brown shale associated with a coal bed about 3 m below US 840.

Region 8

This region is the Poplar River Mine in 2003 and 2004.

US 842: 8A, Poplar River Mine site

N 49° 16.057 W 105° 29.369

These specimens come from the wall of the northern-most trench in 2004. Similar localities likely can be discovered as long as the mining occurs.

Region 9

This region occurs to the east of region 6 along the south wall of the Valley. These areas are accessible only through special permission. The owner of the land, Mr. McCuaig, is wary of scientists due to poor experiences during ecological surveys, particularly of burrowing owls.

US 843: 9A, McCuaig

N 49° 13.005 W 105° 02.275

Shale beds approximately at the base of the Ravenscrag Formation.

US 844: 9B

The Iron Stone beds just above US 843 that are full of *Paloreodoxites*. Again, caution is strongly advised if collecting is to occur.

Localities by township

Rural Municipality of Bengough No. 40

The most northerly Rural Municipality studied in this project, localities in this map area are in locality regions 2, 3 and 9. This map is available in Bengough.

Rural Municipality of Coronach No. 11

This is the township that includes the Poplar River mine (region 8) as well as region 7. The exposures of this area have only been partially explored, as they are difficult to link stratigraphically to the Big Muddy Valley and are rather distant from Bengough. This study did not ascertain the extent of exposure in this area, although anecdotally it is less than that of the Big Muddy Valley. The RM map is available in Coronach.

Rural Municipality of Happy Valley No. 40

This map covers the south of the valley corresponding to the RM of Bengough map. It covers region 1, region 5, region 6, parts of region 9. The RM map is available in Big Beaver.

Rural Municipality of Gladmar No. 9

The area east of Big Beaver is sparsely populated. Region 4 is present in this map area. There is more exposure, but because this region is distant from the other localities this exposure has not been explored. The exposure seems to cross the USA/Canada border. No collecting occurred in the USA during this project. However, some of the beds may prove useful to these purposes. The laws of Montana vary from Saskatchewan in regards to fossil collecting, and would need to be observed in this case. The RM map is available in Gladmar.

APPENDIX C

Measured Sections

These were presented graphically as figs. 5-9. Numbers are thicknesses in m.

1E (US 821)

2	Coarse sandstone, iron stone cap
0.2	Fine sandstone
0.01	Iron stone
0.5	Coaly shales
1.5	Loose silt
0.6	Yellow organic shale w/ coals
1	Poorly consolidated brown silty mudstone
0.4	Dark grey paper shale
0.7	Grey siltstone
2	Medium sandstone
0.2	Sandstone cap (cement)
2	Loose silt/mud trans to fine sandstone iron stone cap
0.7	Grey shale (coal, fossils, brittle)
1.5	Loose sand
2	Sandstone w/ siltstone interbedding
0.3	Iron stone (clay sized matrix, fossils)
1	Grey brown siltstone w/0.1 coal in middle
0.5	Coal (solid)
0.7	Grey mudstone
1.5	Yellow grey banded sandy siltstone
0.05	Iron stone
1	Yellow siltstone w/ sandy layers
0.4	Grey silty shale
0.5	Yellow shale, numerous microcoals
0.6	Brown silty shale
1.7	Paper shale w/2 notable coals
0.6	Brown silty shale
0.2	Organic shale
0.01	Coal
0.9	Dark brown grey siltstone/shale
0.5	Grey siltstone w/thin coals
0.1	Grey shale
0.6	Tan sandy siltstone
1.1	Grey brown siltstone
0.3	Siltstone w/ fine sand nodules, iron stone cap
1.2	Grey brown siltstone w/ fossils (ghost), iron ston, thin iron stone cap

1C (US 819)

8	Coarse sandstone, hard
3.5	Sand
0.5	Mud
0.6	Coal interbeds
0.2	Mud
3.9	Coarse to fine sand
0.01	Iron stone
0.4	Coarse sandstone, hard
0.1	Coal
0.8	Mudstone
0.1	Coal
1.5	Siltstone
0.05	Iron stone
2.7	Siltstone
0.3	Coaly shales, fossils (poor)
0.01	Coal
0.8	Fine sandstones
4.5	Medium sandstone
1.1	Brown mudstone
0.1	Fine sandstone
0.1	Iron stone
0.5	Yellow siltstone
0.4	Laminated shale
0.01	Coal
0.8	Loose Mud
1.5	Grey shale w/ fossils (poor)
0.5	Organic rich shale
0.7	Brown siltstone with sandy layers
0.01	Coal
0.9	Green-grey siltstone
0.1	Iron stone
1.3	Silt w/Iron stone beds
0.6	Triple coal (Boundary coal)
3.5	White siltstone
1.1	Organic siltstone
1.7	Grey siltstone
1	Fine sandstone
0.5	Organic siltstone
0.9	Grey siltstone
0.5	Organic siltstone
0.7	Grey siltstone
0.5	Organic siltstone

2A (US 822)

0.01	Iron stone
1.6	Brown-grey siltstone
2	Loose silt w/microcoals
1.2	Grey-brown siltstone
0.2	Loose silt
0.3	Coal
0.2	Shales
0.01	Coal
0.4	Silty mudstone
0.6	Shale, fragile, good fossils
0.2	Coal
0.7	Silty Mud (poor consolodation)
0.5	Shale, fossil rich (July 5 coll)
1	Grey silt stone, thin coal at top
1.4	Grey brown sand stone w/ iron stone layers
0.01	Coal
0.6	Grey shale, fossil rich, July 8 collection
0.1	Iron stone
0.5	Fine sand to slitstone, fining upwards
0.4	Triple coal, yellow silt (Boundary coal)
0.5	Medium brown shale
0.7	Light grey siltstone, "chewed" plants
1.7	Orange/white siltstone, blocky, some iron stone
0.2	Organic rich shale
2.1	Dark grey siltstone
2.3	White coarse sandstone, xbeds, fining upwards

2D (US 825)

1	Organic shales
0.6	Clay stone: blocky
1.5	Organic shales w/ coal
1.5	Fine shaley mudstone, fossils
0.2	Coal
1	Loose silty clay
0.01	Coal
1	Brown mudstone, hard
0.01	Coal
1.4	Brown siltstone, Iron stonelayers
0.8	Brown siltstone
0.5	Orange iron rich mudstone
0.9	Grey brown mudstone
0.8	Yellow green mudstone
0.01	Coal
1	Brown siltstone w/ some fossils
0.01	Coal
0.6	Brown silt stone
0.2	Shale: laminated, organic rich
0.3	Siltstone, brown
0.6	Triple coal (Boundary coal)
1.2	Brown grey siltstone
2.2	Grey siltstone
1.5	Organic rich sandy siltstone
1.35	Grey siltstone

6A (US 838)

	Sand
2	Tan silty clay
0.3	Grey brown siltstone
1.5	Tan siltstone
0.3	Coal
1.5	Dark grey siltstone
3	Brown grey siltstone
1	Mudstone w/ sand lenses
0.7	Fine sandstone, small x beds
0.1	Iron stone
1.5	Silty shale w/ coals
0.3	Unconsolidated silt
0.8	Brown shale
1	Coaly shale
1.7	Grey mudstone
2	Brown mudstone
2.5	Grey silt w/ iron stone bands
0.7	Coal
0.2	Organic rich siltstone
0.4	Dark grey siltstone, some iron staining
0.3	Silty clay
0.8	Grey siltstone w/ fossils
0.01	Coal
0.4	Unconsolidated silt, tan
0.3	Tan siltstone
0.5	Unconsolidated silty clay
0.1	Coal
0.8	Grey siltstone-shale w/ fossils
0.5	Shale w/ fossils, coarsening upwards to fine sand
0.5	Coal
1	Grey siltstone
2.2	Brown silty clay
0.2	Organic rich shale
0.2	Coal
0.7	Shale-siltstone (coarsening upwards)
0.3	Coal
1	Brown grey silty clays
0.1	Shale
1	Grey mudstone w/ great fossils
0.1	Paper shale
0.4	Coal
1	Siltstone w/ sandy parts
1	Siltstone w/ sand and shales
0.1	Paper shale
2	Coarse sand - siltstone, fining upwards

1.6	Fine sandstone w/ silt, fossils
0.1	Paper shale
0.2	Coal
2.3	Grey brown siltstone w/ iron stone, sandy parts, structure (wavy beds), lenses and channels?
0.2	Dark grey siltstone
0.2	Shale
0.8	Siltstone w/ some fossils
0.4	Unconsolidated mud
0.2	Shale
0.4	Coal
0.2	White silty clay
0.4	Coal
1.8	Shales w/ coals, organic rich, poor fossils
0.01	Coal
1	Organic rich silt
2.1	White and medium grey sand stone, some silt layers, root fossils

Plate 1

Figure 1. cf. *Isoetites horridus* (Dawson) Brown, sterile leaves, US817-9008. Scale bar = 1cm.

Figure 2. *Equisetum* sp., sterile axes, US842-9009. Scale bar = 1cm.

Figure 3. cf. *Woodwardia gravida* Hickey, Sterile pinnules, US820-9010. Scale bar = 1cm.

Figure 4. *Onoclea hesperia* Brown, sterile pinnule, US830-9011. Scale bar = 1cm.

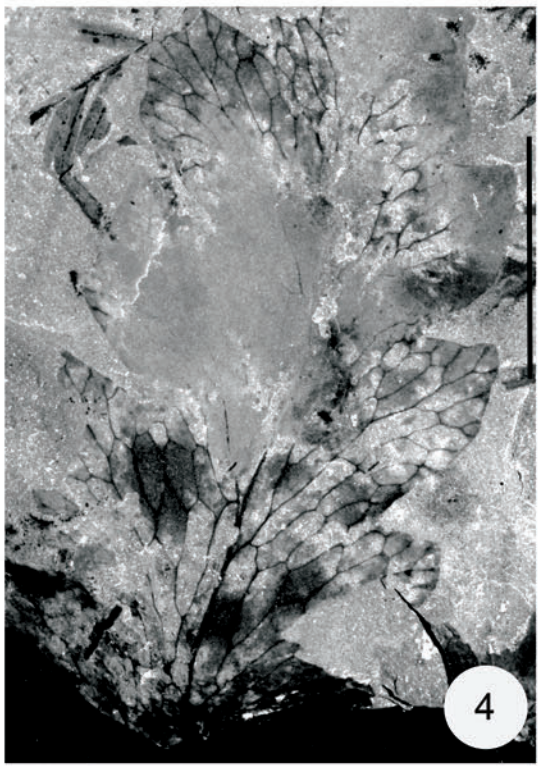


Plate 1

Plate 2

Figure 1-2. *Dennstaedtia americana* Knowlton.

Figure 1. Sterile pinnule, US832-9012. Scale bar = 1cm.

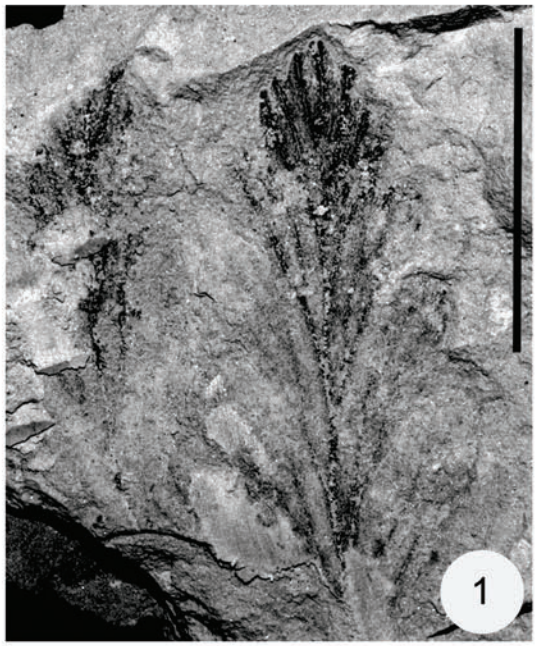
Figure 2. Fertile pinnule, arrow points to sorus, US832-9013. Scale bar = 1cm.

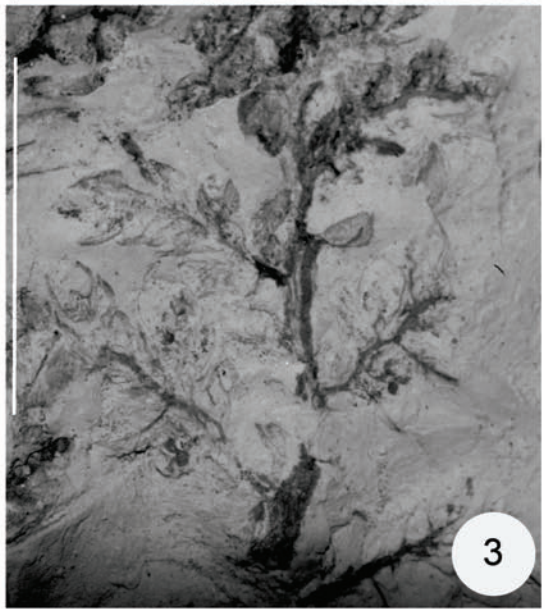
Figure 3-4. *Azolla schopfii* Dijkstra.

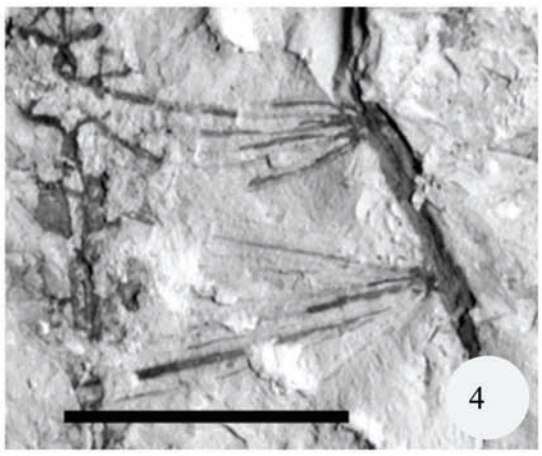
Figure 3. Axis showing branching, US840-9014. Scale bar = 1cm.

Figure 4. Root bundles, US840-9015. Scale bar = 1cm.

Figure 5. cf. *Azolla vellus* (Dijkstra) Jain & Hall, US845-9016. Scale bar = 1cm.







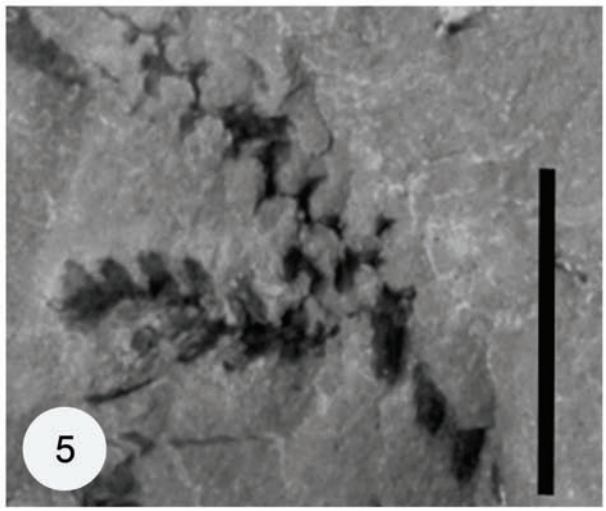


Plate 2

Plate 3

Figure 1-4. *Lygodium* sp.

Figure 1. Leaves arising from a larger axis, US834-9017. Scale bar = 1cm.

Figure 2. Non-linear leaves, US834-9018. Scale bar = 1cm.

Figure 3. Leaves with compound serrate margins, US834-9019. Scale bar = 1cm.

Figure 4. Additional leaf morphologies, US834-9020. Scale bar = 1cm.

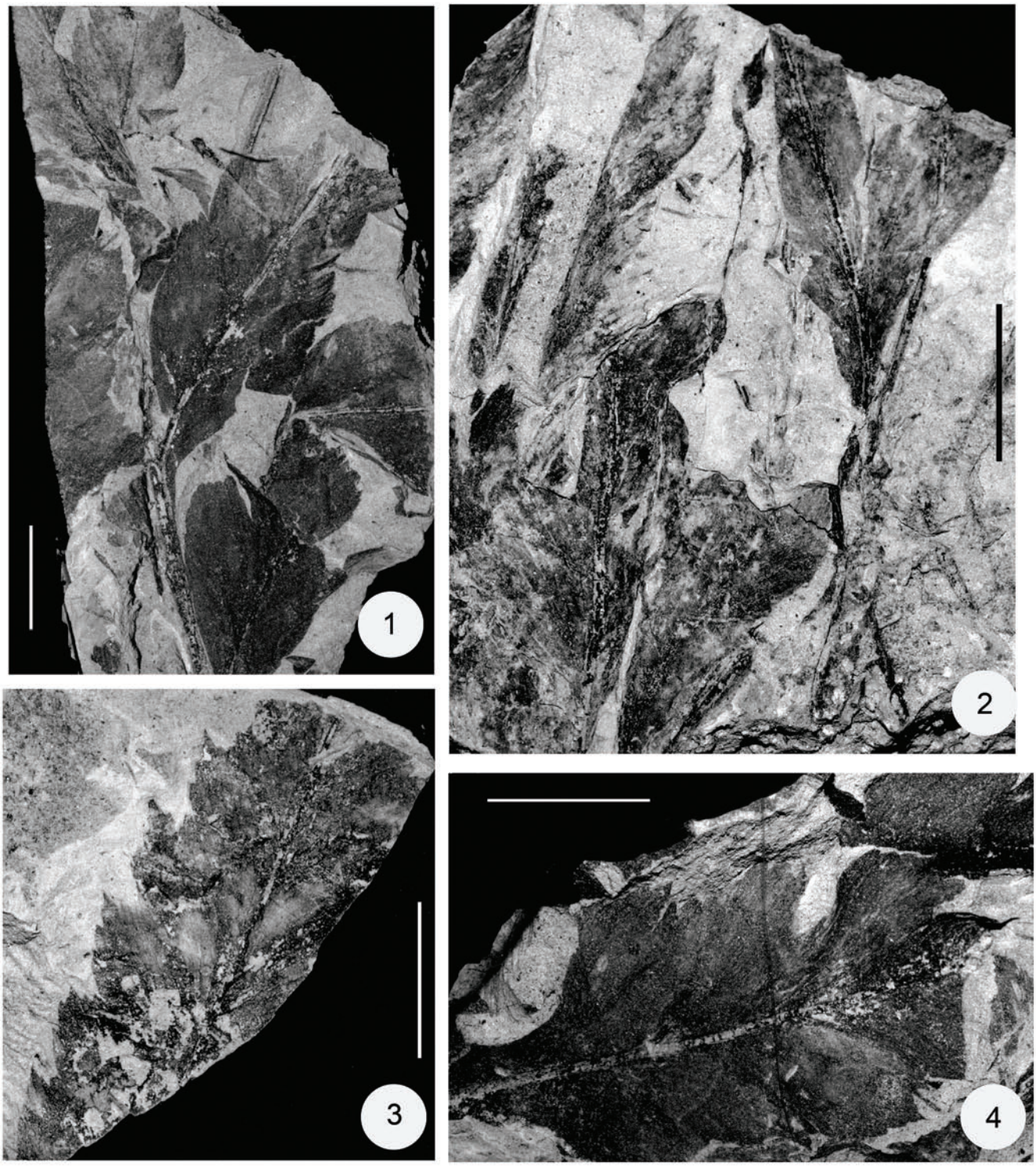


Plate 3

Plate 4

Figure 1-2 *Thelypteris* sp.

Figure 1. Sterile pinna fragment, US817-9021. Scale bar = 1cm.

Figure 2. Fertile pinna fragment, US817-9022. Scale bar = 1cm.

Figure 3. Unknown Fern, arrow points to *Browneia serrulata* capsule, US817-9023. Scale bar = 1cm.

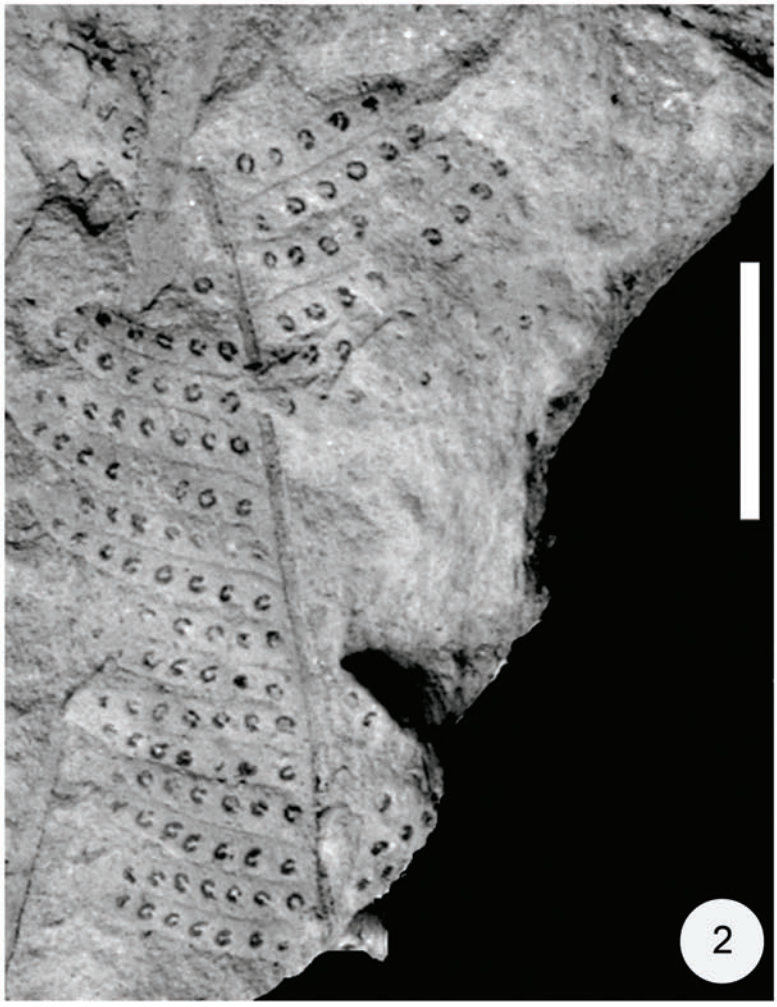


Plate 4

Plate 5

Figure 1-8. *Glyptostrobus dakotensis* Brown.

Figure 1. Foliage, US817-9024. Scale bar = 1cm.

Figure 2. Seed cones on axis, US820-9025. Scale bar = 1cm.

Figure 3. Seed cone, US821-9026. Scale bar = 1cm.

Figure 4. Seed cone scale, US838-9027. Scale bar = 1cm.

Figure 5. Seed cone, US840-9028. Scale bar = 1cm.

Figure 6. Seed, US817-9029. Scale bar = 1cm.

Figure 7. Seed cone attached to branch, US817-9030. Scale bar = 1cm.

Figure 8. Seed cone scale and foliage, US828-9031. Scale bar = 1cm.

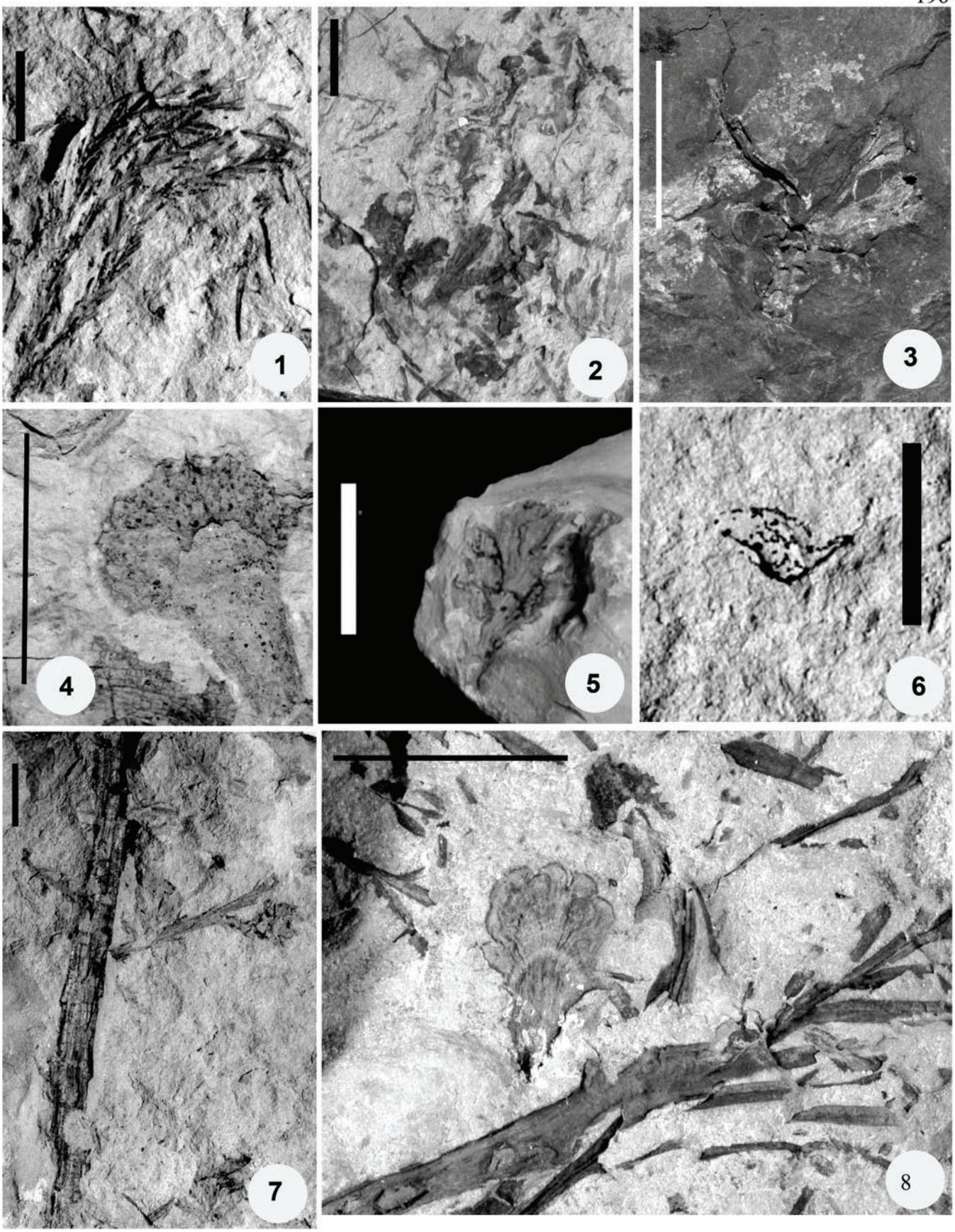


Plate 5

Plate 6

Figure 1-3. *Metasequoia occidentalis* (Newberry) Chaney.

Figure 1. Cone, US843-9032. Scale bar = 1cm.

Figure 2. Cone, US828-9033. Scale bar = 1cm.

Figure 3. Foliage, US843-9034. Scale bar = 1cm.

Figure 4-5. *Elatocladus megasequoiae* sp. nov.

Figure 4. Foliage (Holotype), US828-9035. Scale bar = 1cm.

Figure 5. Foliage, US828-9036. Scale bar = 1cm.

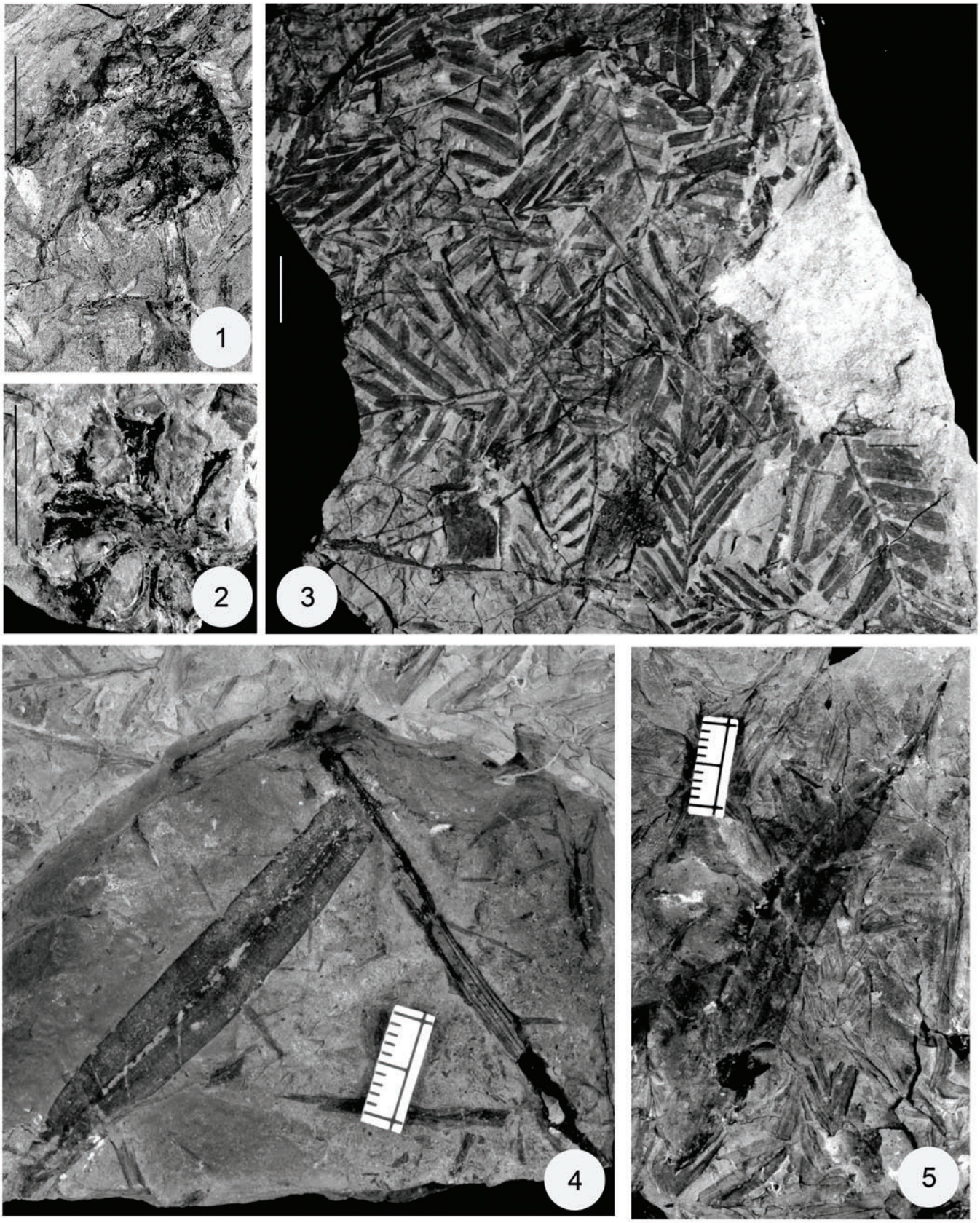


Plate 6

Plate 7

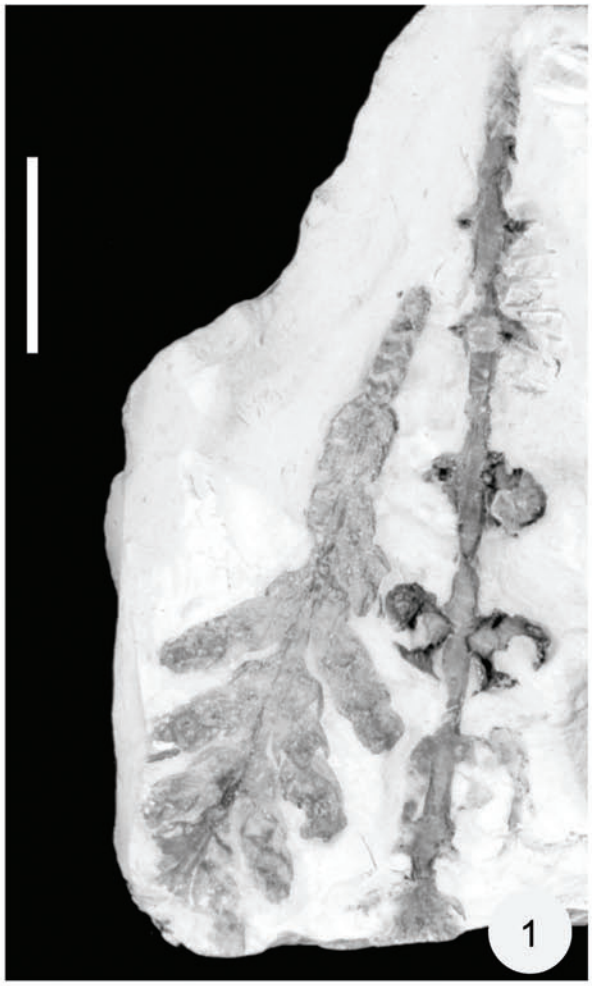
Figure 1-4. *Mesocyparis borealis* McIver and Basinger.

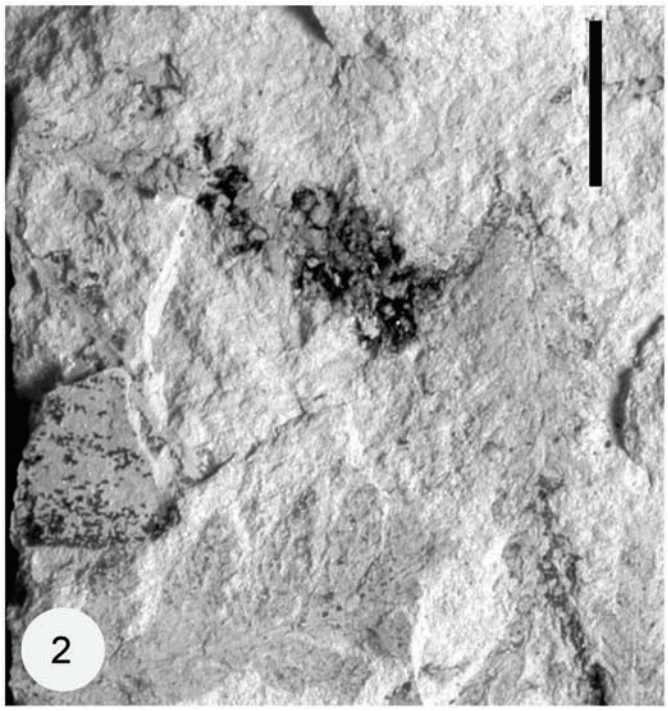
Figure 1. Foliage and seed cones, US840-9037. Scale bar = 1cm.

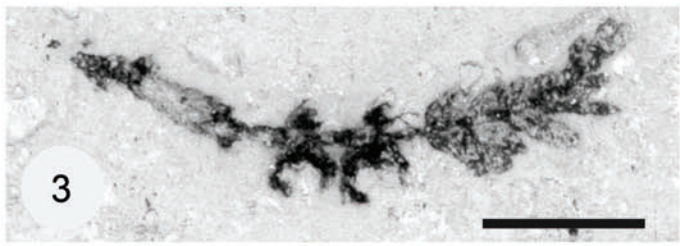
Figure 2. Foliage and seed cones, US826-9038. Scale bar = 1cm.

Figure 3. Foliage and seed cones, US832-9039. Scale bar = 1cm.

Figure 4. Foliage and seed cones, US840-9040. Scale bar = 1cm.







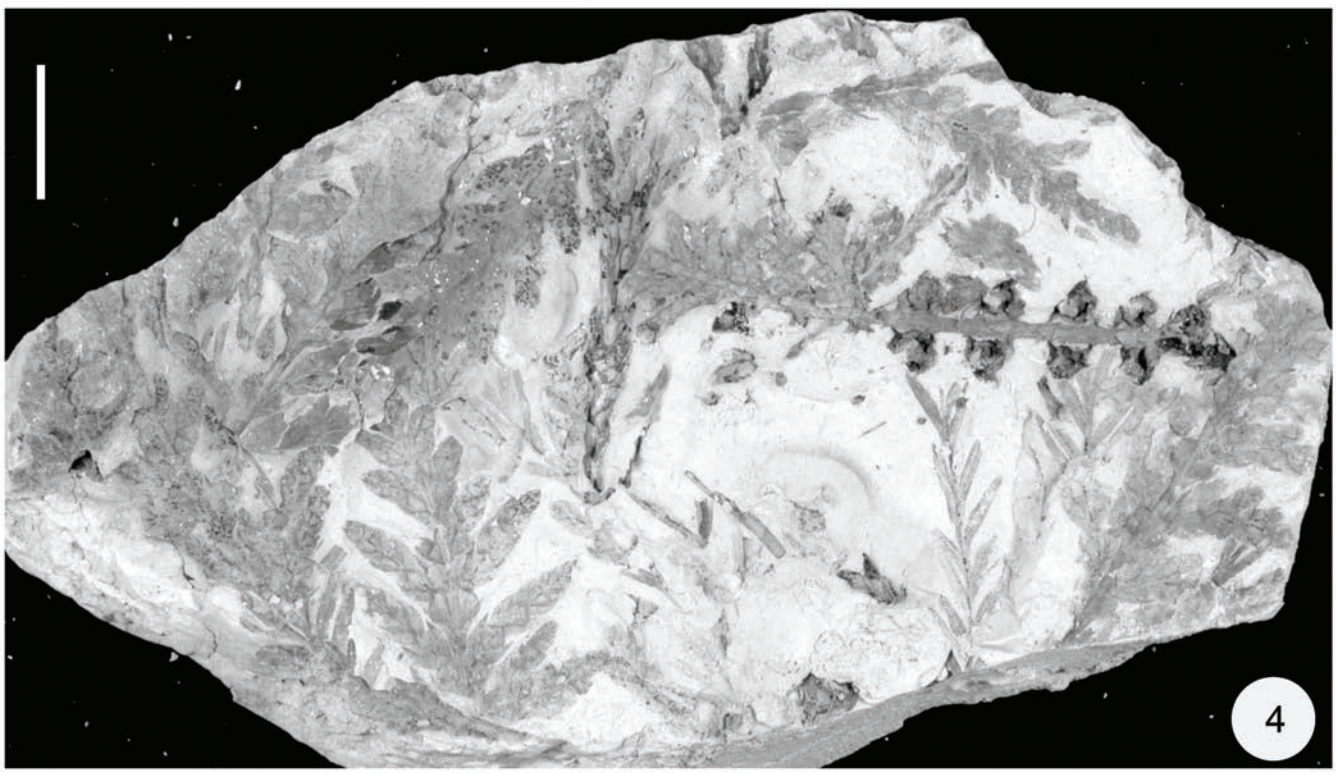


Plate 7

Plate 8

Figure 1-6. *Corvirupestrobus adrielensis* gen. et sp. nov.

Figure 1. Cone (Holotype), US840-9041. Scale bar = 1cm.

Figure 2. Cone, US840-9042. Scale bar = 1cm.

Figure 3. Cone, US840-9043. Scale bar = 1cm.

Figure 4. Cone, US840-9044. Scale bar = 1cm.

Figure 5. Cone, US840-9045. Scale bar = 1cm.

Figure 6. Cone, US822-9046. Scale bar = 1cm.

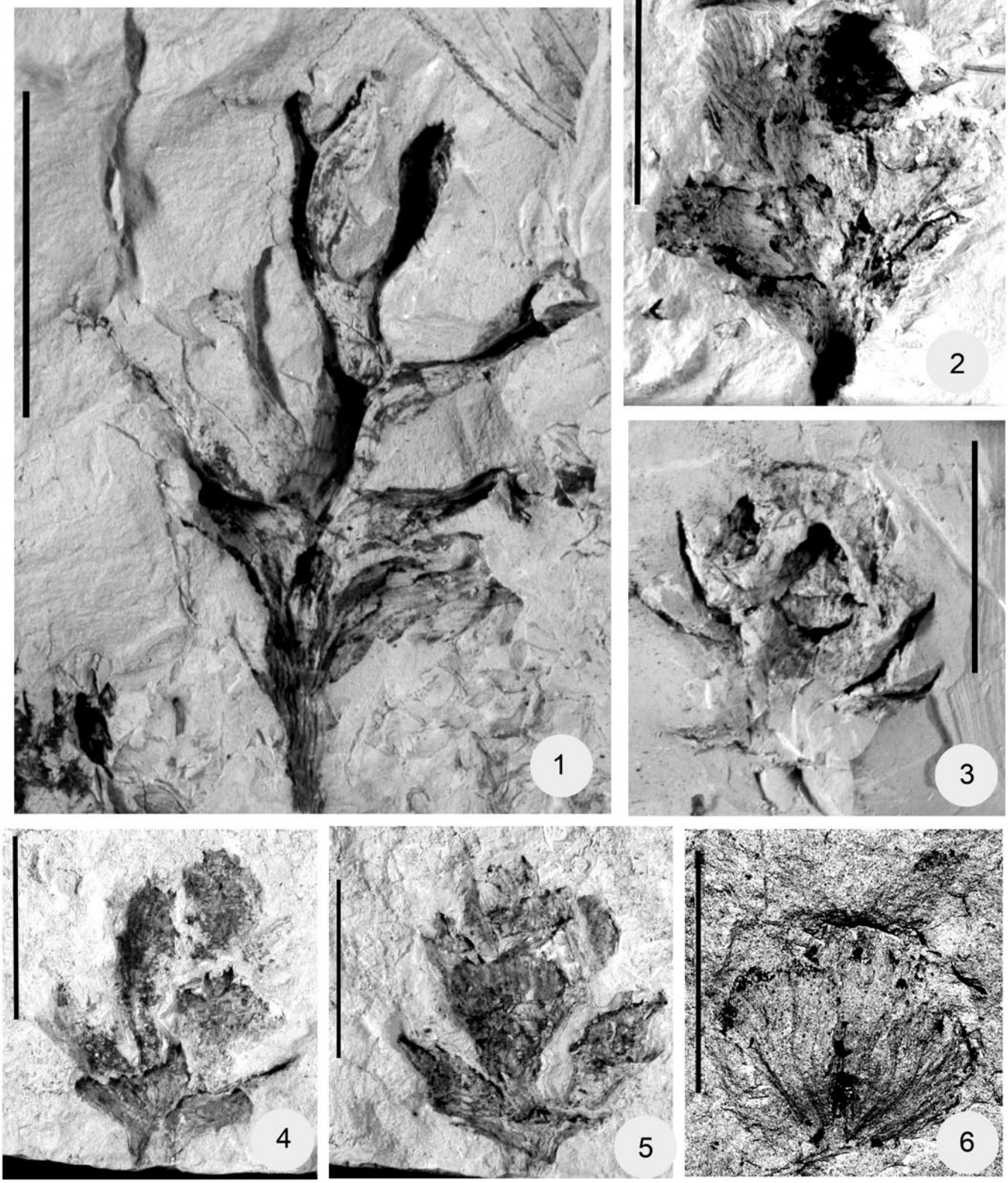


Plate 8

Plate 9

Figure 1-2. *Sparganium* sp.

Figure 1. Inflorescence, US832-9047. Scale bar = 1cm.

Figure 2. Inflorescence, US832-9048. Scale bar = 1cm.

Figure 3. Unknown monocot leaves, US832-9049. Scale bar = 1cm.

Figure 4. *Paloreodoxites plicatus* (Lesquereux) Knowlton, leaves, US844-9050. Scale bar = 1cm.

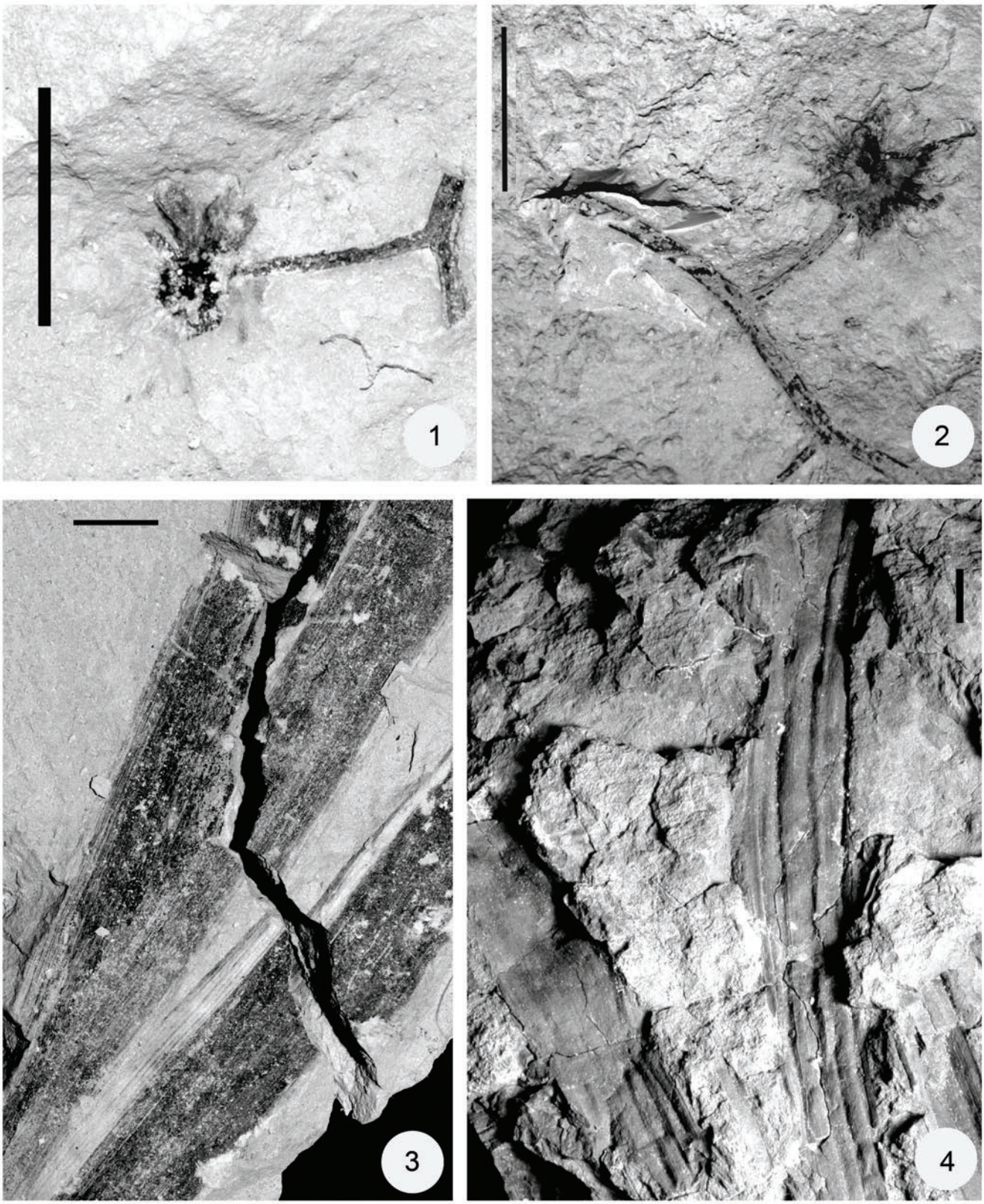


Plate 9

Plate 10

Figure 1-3. *Paranymphaea crassifolia* (Newberry) Berry.

Figure 1. Complete leaf, US845-9051. Scale bar = 1cm.

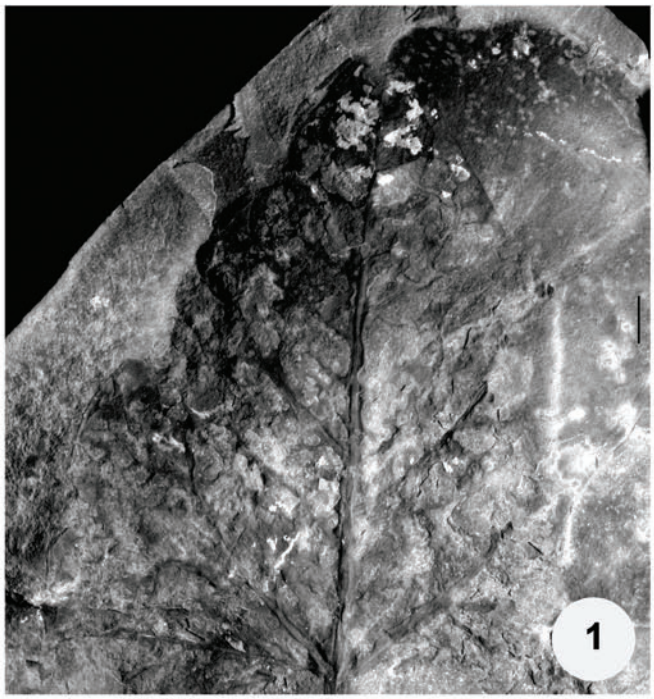
Figure 2. Marginal portion of a leaf, US822-9052. Scale bar = 1cm.

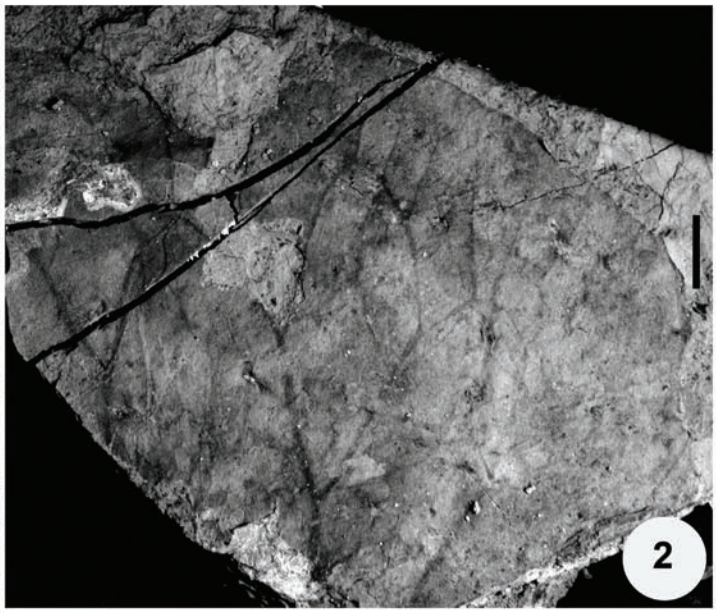
Figure 3. Marginal portion of a leaf and ambiguous structure, US822-9053. Scale bar = 1cm.

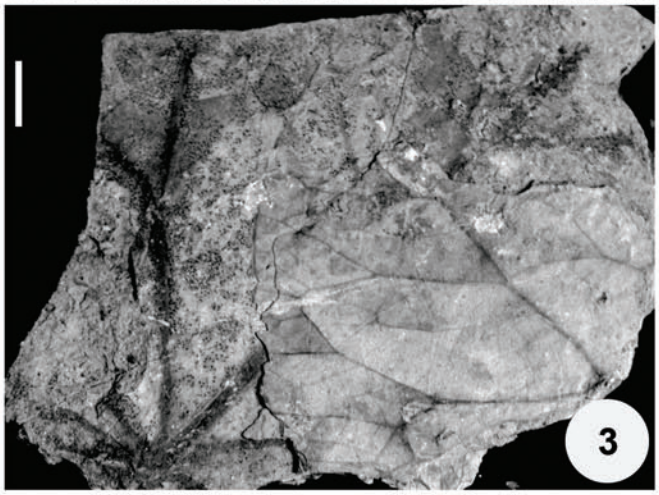
Figure 4-5. *Nelumbago montanum* (Brown) McIver and Basinger.

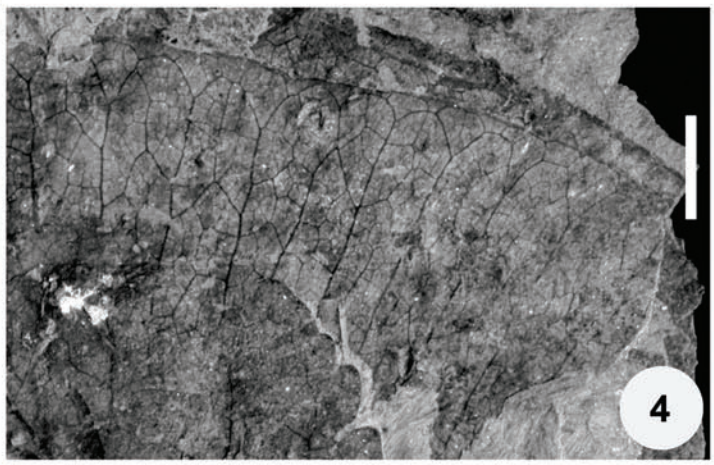
Figure 4. Leaf fragment, US822-9054. Scale bar = 1cm.

Figure 5. Leaf fragment with diameter, US822-9055. Scale bar = 1cm.









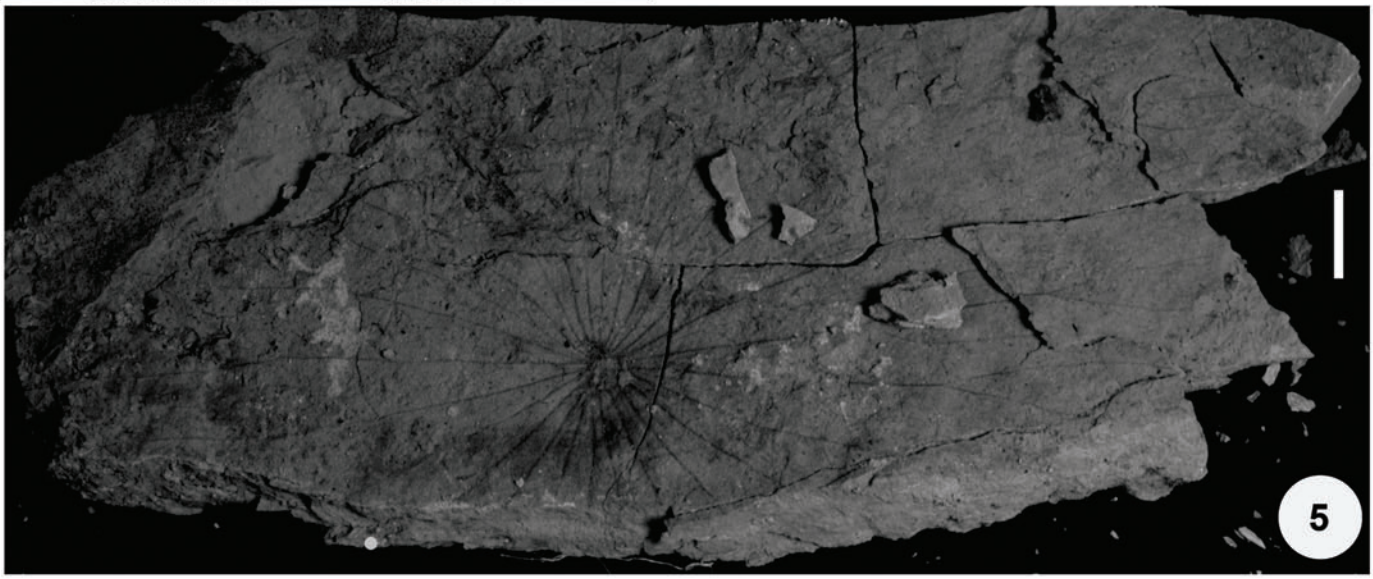


Plate 10

Plate 11

Figure 1-2. *Ettingshausenia raynoldsii* (Newberry) Moiseeva.

Figure 1. Leaf, US828-9056. Scale bar = 1cm.

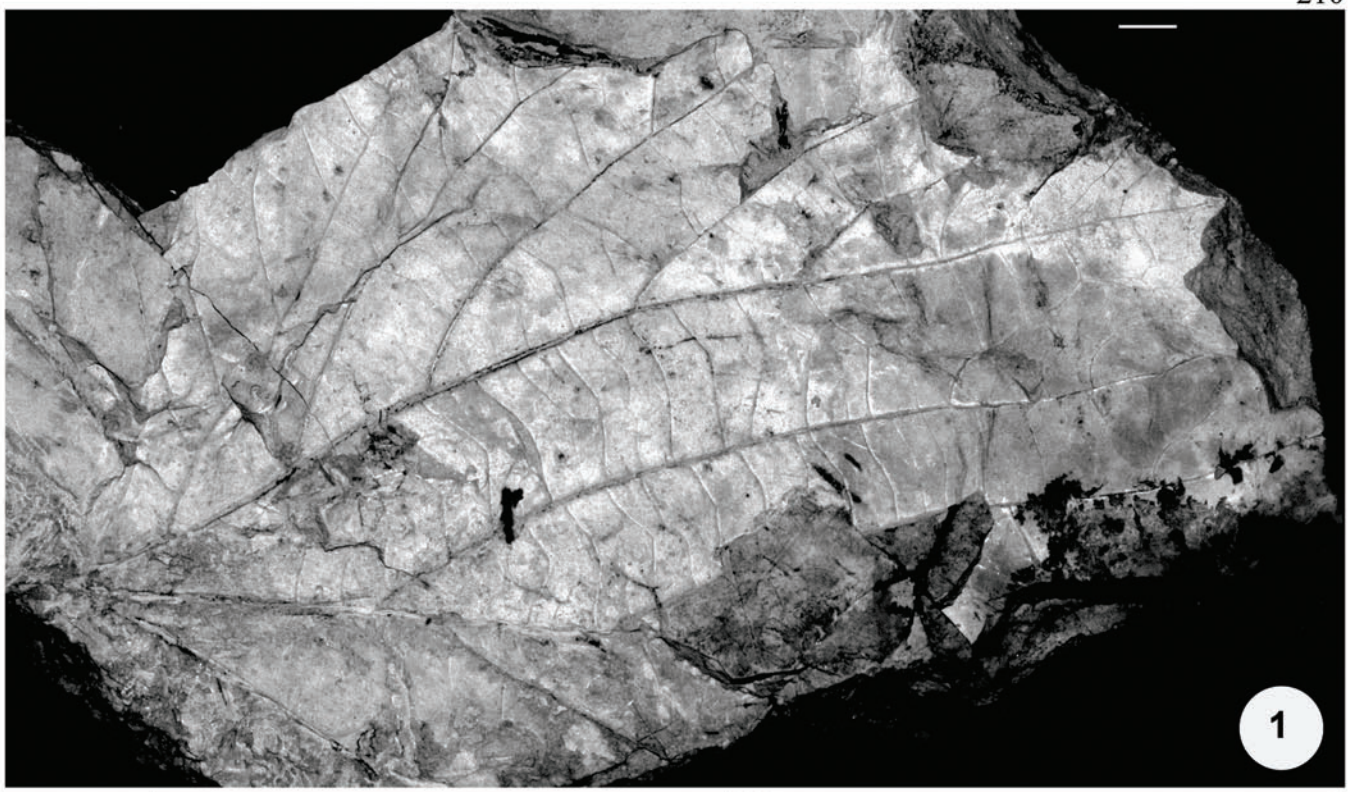
Figure 2. Leaf tip, US828-9057. Scale bar = 1cm.

Figure 3-5. *Macginicarpon* sp.

Figure 3. Inflorescence, US834-9058. Scale bar = 1cm.

Figure 4. Inflorescence, US834-9059. Scale bar = 1cm.

Figure 5. Inflorescence, US834-9060. Scale bar = 1cm.



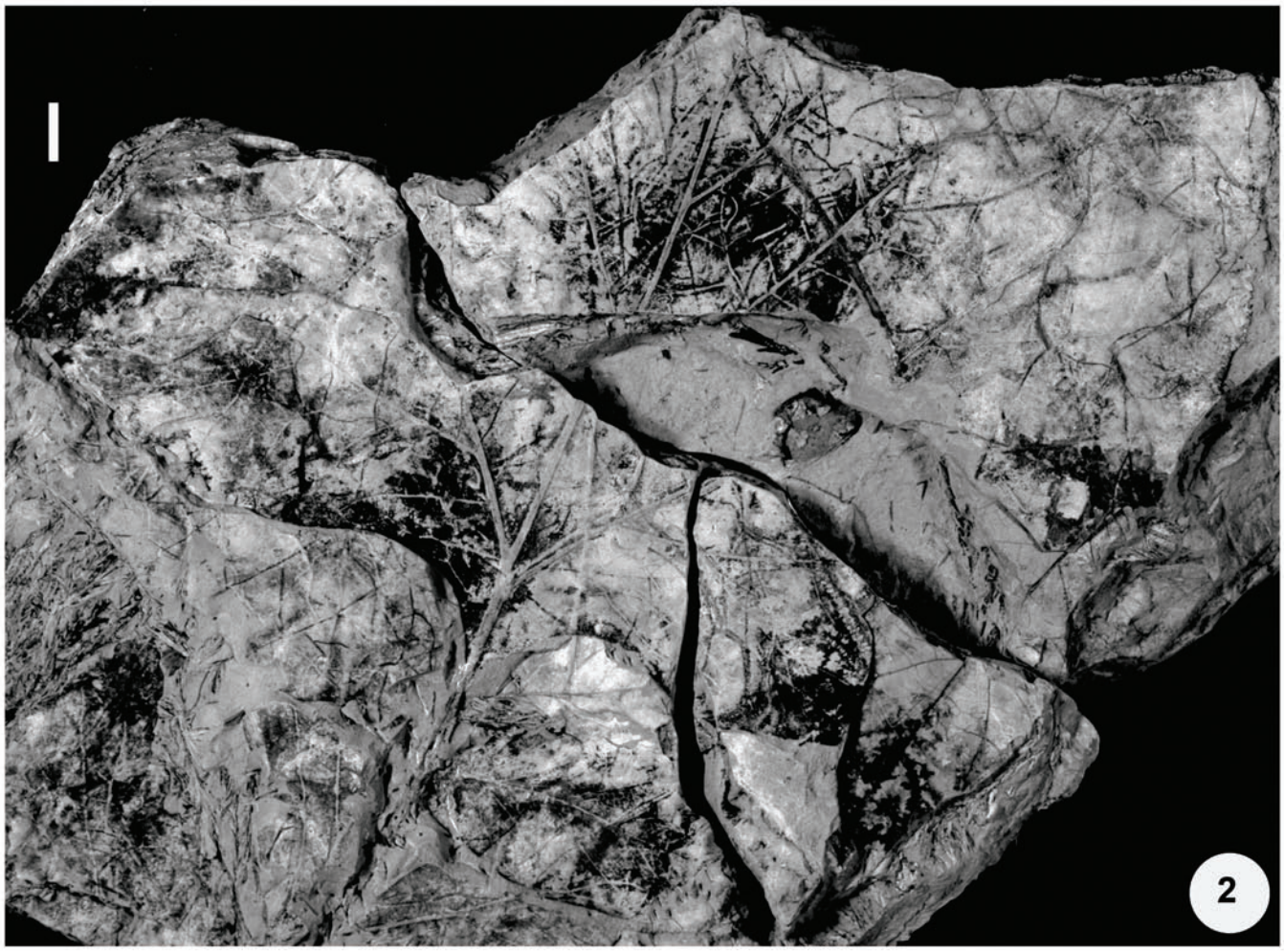


Plate 12

Plate 13

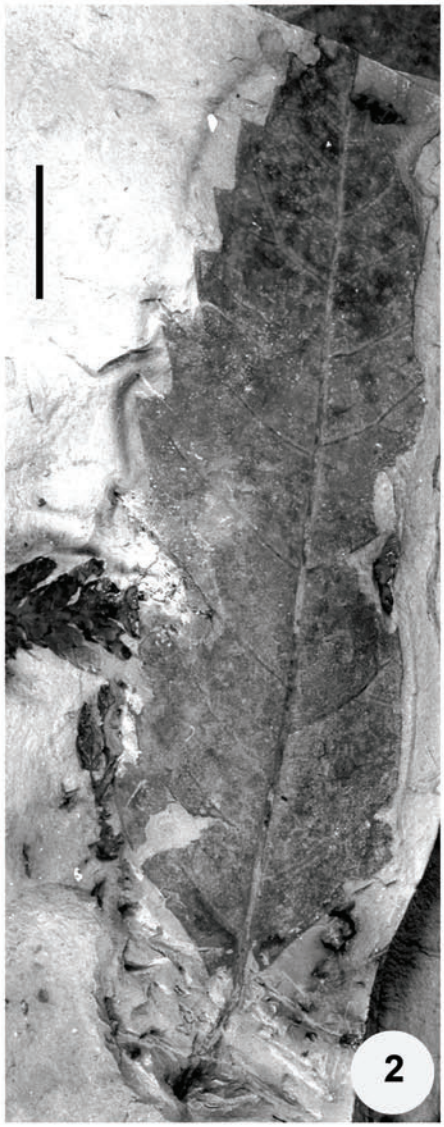
Figure 1-4. *Fagopsiphyllum praegroenlandicum* (Berry) comb. nov.

Figure 1. Leaf, showing venation, US840-9063. Scale bar = 1cm.

Figure 2. Complete leaf including petiole, US840-9064. Scale bar = 1cm.

Figure 3. Leaf, US822-9065. Scale bar = 1cm.

Figure 4. Leaf, US840-9066. Scale bar = 1cm.



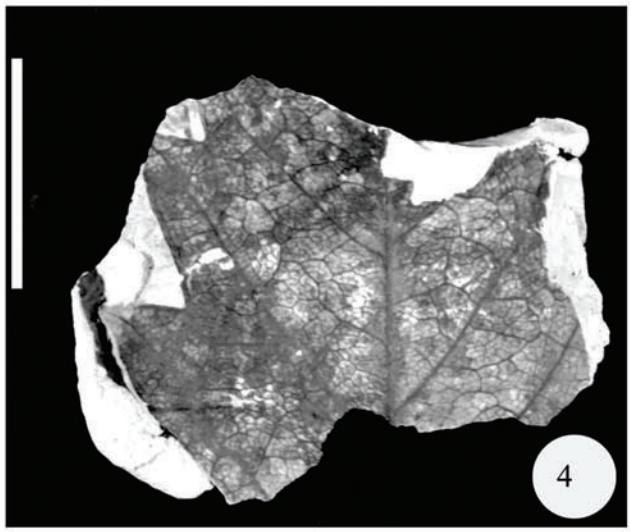


Plate 13

Plate 14

Figure 1-4. *Carya antiquorum* Newberry.

Figure 1. Leaflet, US832-9067. Scale bar = 1cm.

Figure 2. Leaflet, US832-9069. Scale bar = 1cm.

Figure 3. Leaflet, US832-9070. Scale bar = 1cm.

Figure 4. Leaflet, US832-9071. Scale bar = 1cm.

Figure 5. *Aesculus hickeyi* Manchester, leaf, from Estevan area, US28-9072. Scale bar = 1cm.

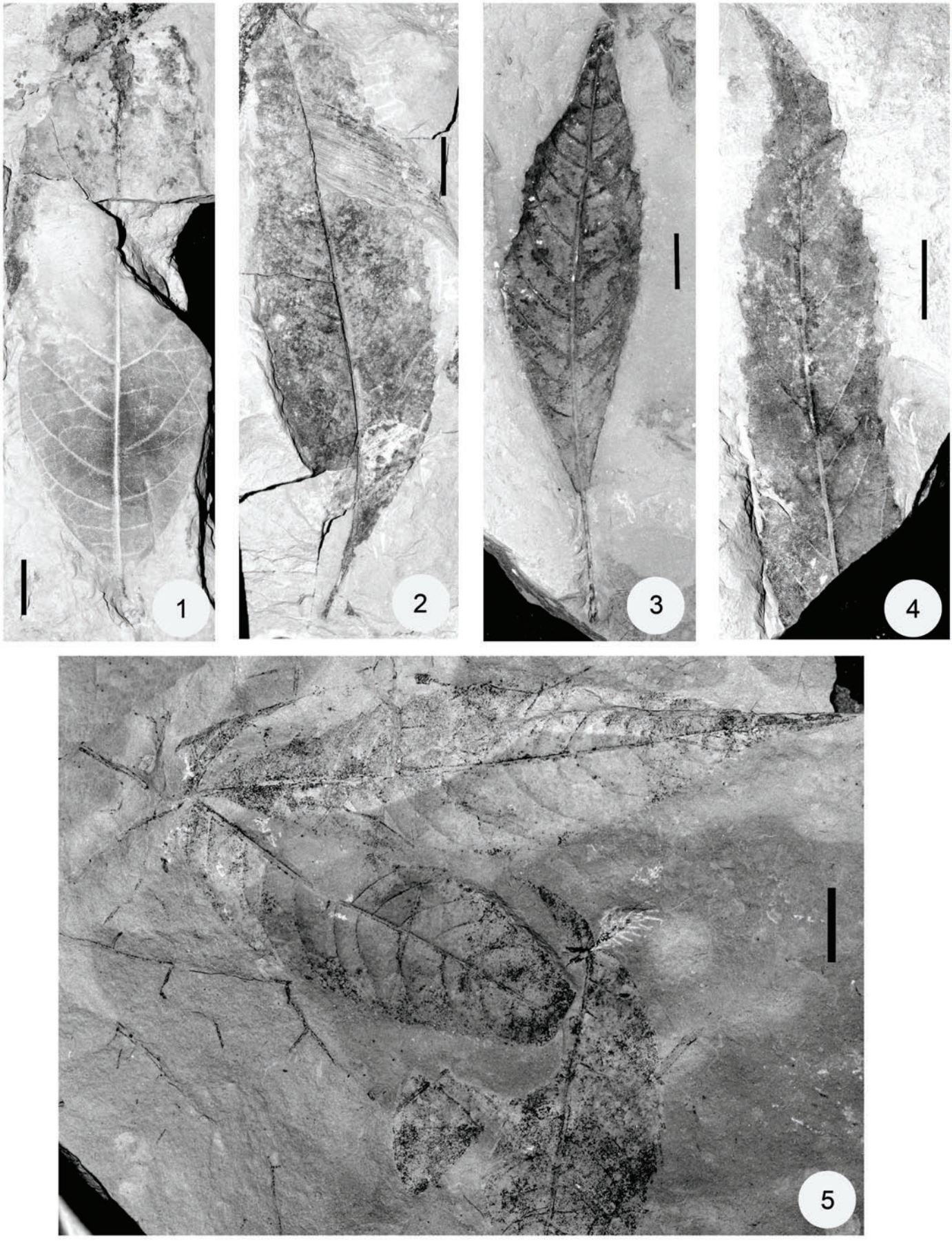


Plate 14

Plate 15

Figure 1-4. *Trochodendroides speciosa* (Ward) Berry.

Figure 1. Leaf, US826-9073. Scale bar = 1cm.

Figure 2. Leaf, US822-9074. Scale bar = 1cm.

Figure 3. Smallest leaf, US834-9075. Scale bar = 1cm.

Figure 4. Leaf, US834-9076. Scale bar = 1cm.

Figure. 5-6. *Nyssidium arcticum* (Heer) Iljinskaja.

Figure 5. Complete axis, US932-9077. Scale bar = 1cm.

Figure 6. Isolated fruit, US834-9078. Scale bar = 1cm.

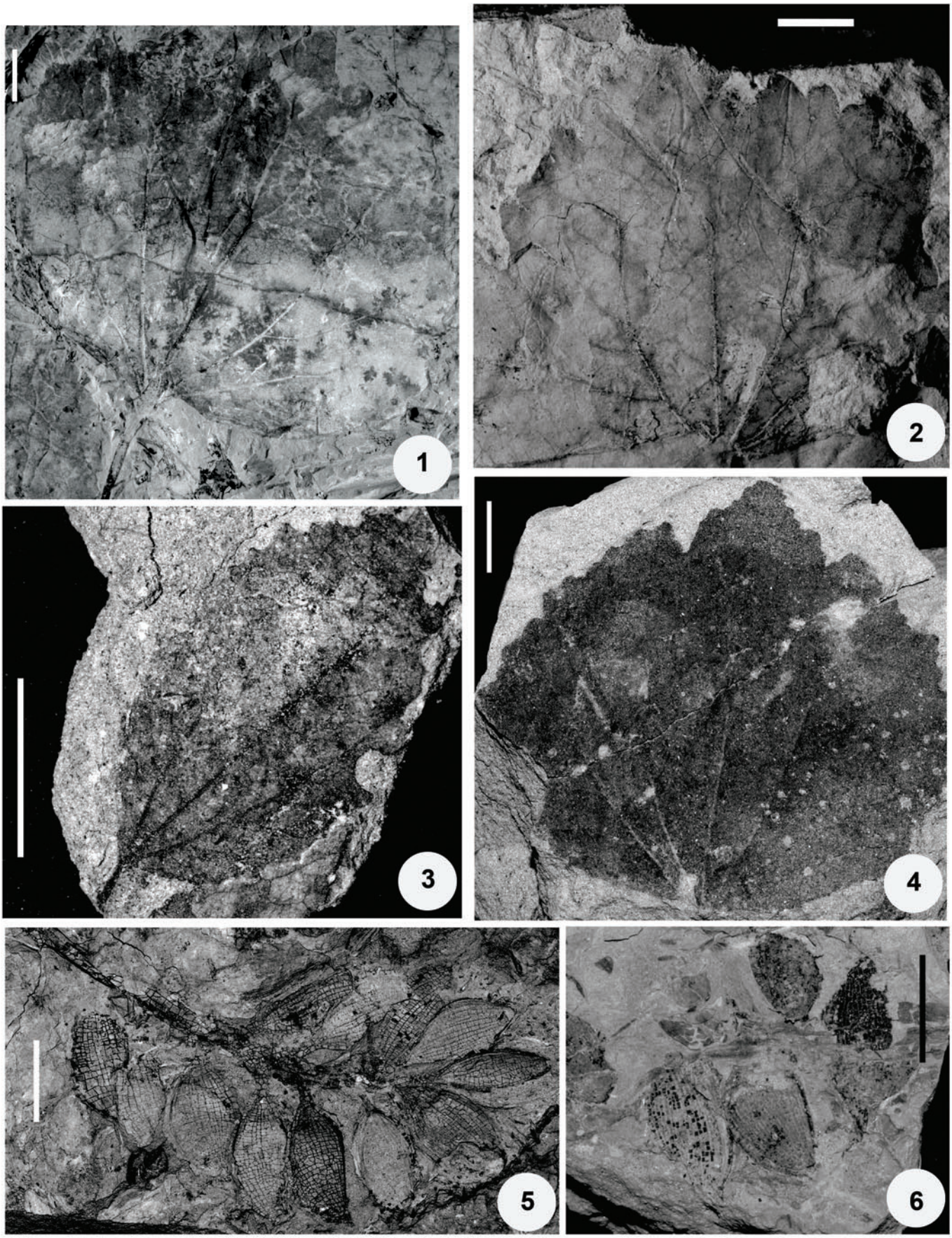


Plate 15

Plate 16

Figure 1-3, 5. *Zyziphoides flabella* Crane, Manchester and Dilcher.

Figure 1. Leaf, US822-9079. Scale bar = 1cm.

Figure 2. Leaf, US830-9080. Scale bar = 1cm.

Figure 3. Leaf, US822-9081. Scale bar = 1cm.

Figure 5. Leaf, US822-9083. Scale bar = 1cm.

Figure 4, 6. *Nordenskioldia borealis* Heer

Figure 4. Single fruit, US830-9082. Scale bar = 1cm.

Figure 6. Single fruit, US830-9084. Scale bar = 1cm.

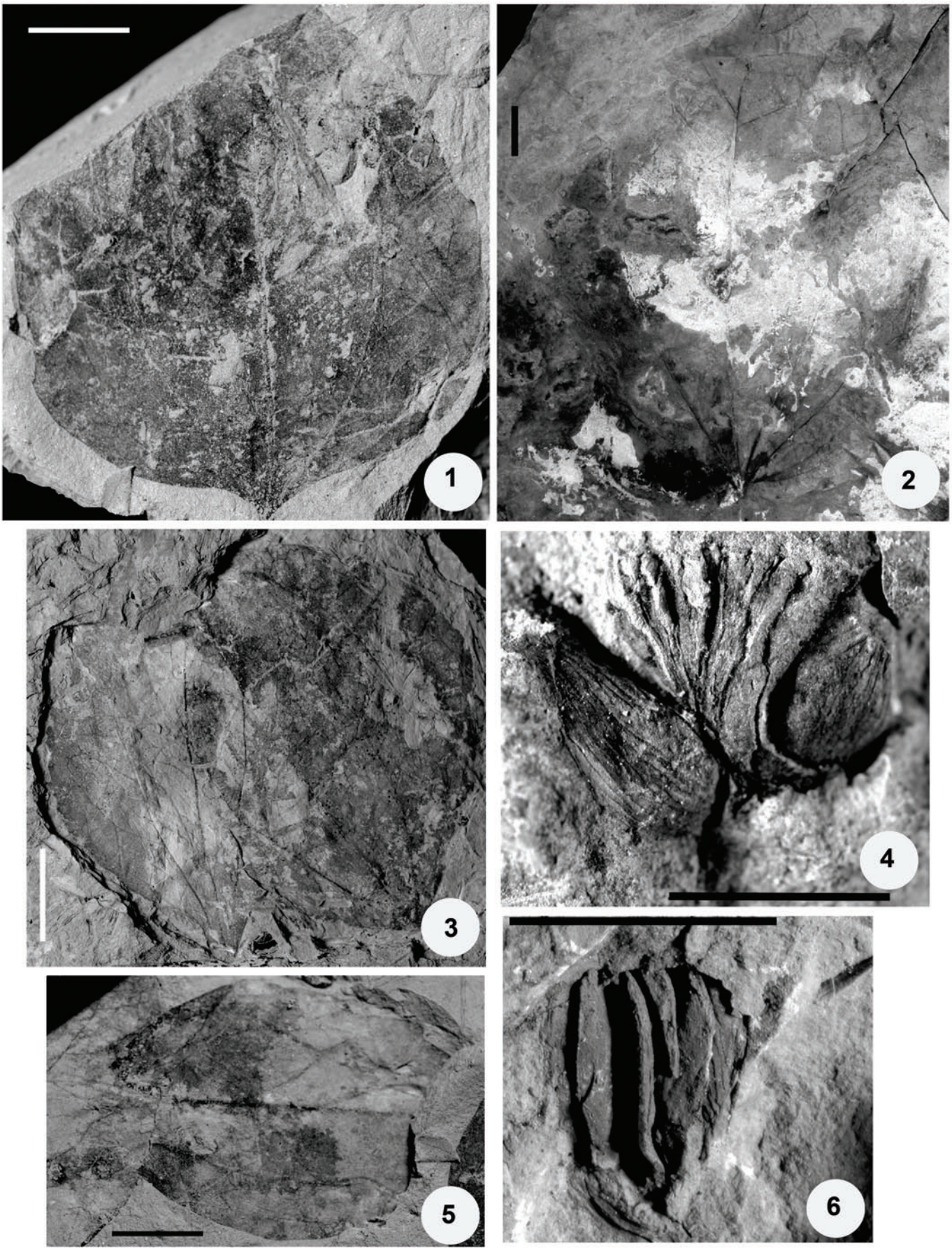


Plate 16

Plate 17

Figure 1. *Nordenskioldia borealis* Heer, fruits on axis, US830-9085. Scale bar = 1cm.

Figure 2-4. *Archeampelos acerfolia* (Newberry) McIver and Basinger.

Figure 2. Complete leaf, US817-9086. Scale bar = 1cm.

Figure 3. Complete leaf, US817-9087. Scale bar = 1cm.

Figure 4. Leaf Base, US817-9088. Scale bar = 1cm.

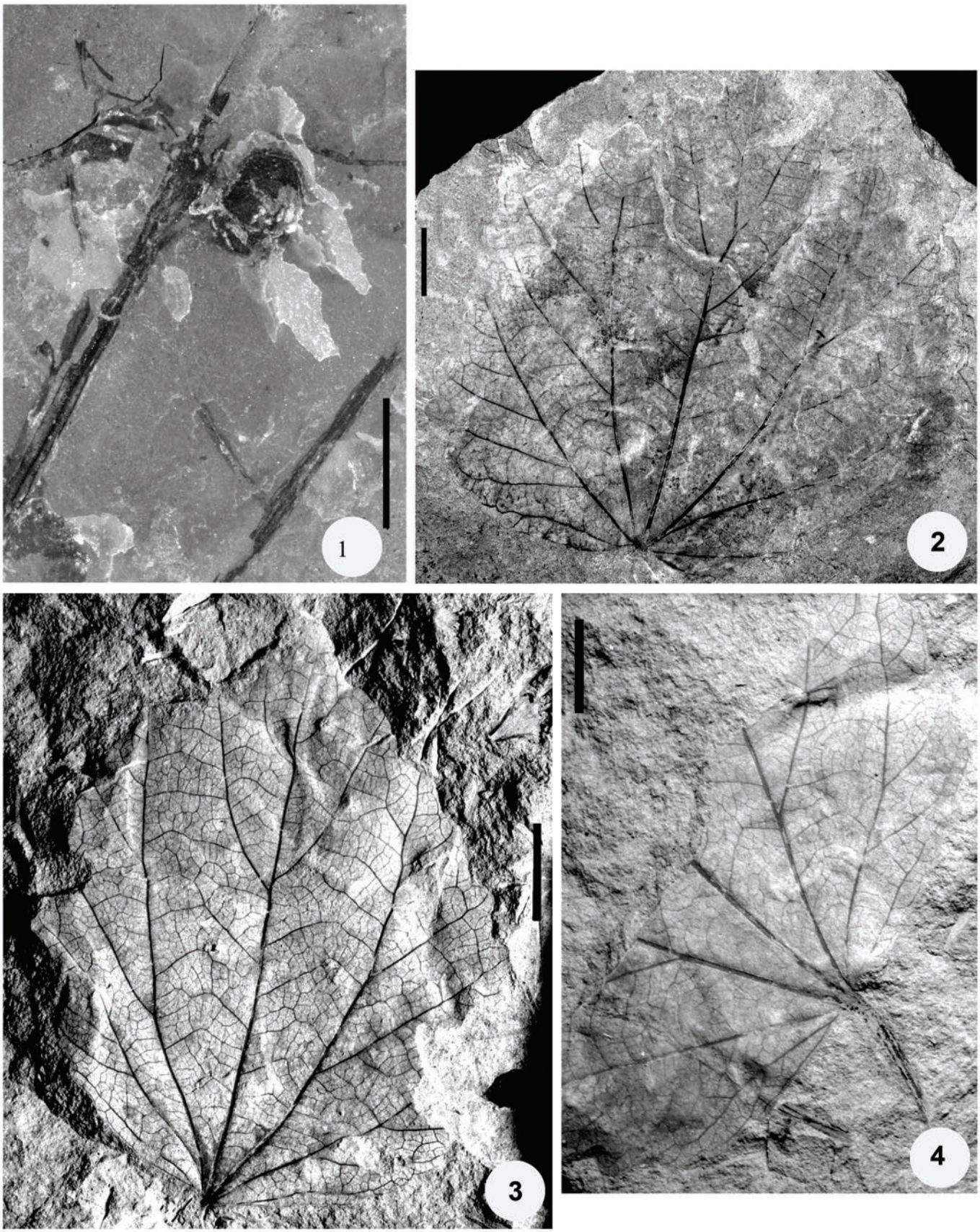


Plate 17

Plate 18

Figure 1-4. *Browneia serrulata* (Newberry) Manchester and Hickey.

Figure 1. Leaf, US840-9089. Scale bar = 1cm.

Figure 2. Leaf, arrow indicating a bivalve, US830-9090. Scale bar = 1cm.

Figure 3. Leaf base, US840-9091. Scale bar = 1cm.

Figure 4. Leaf margin, US830-9092. Scale bar = 1cm.

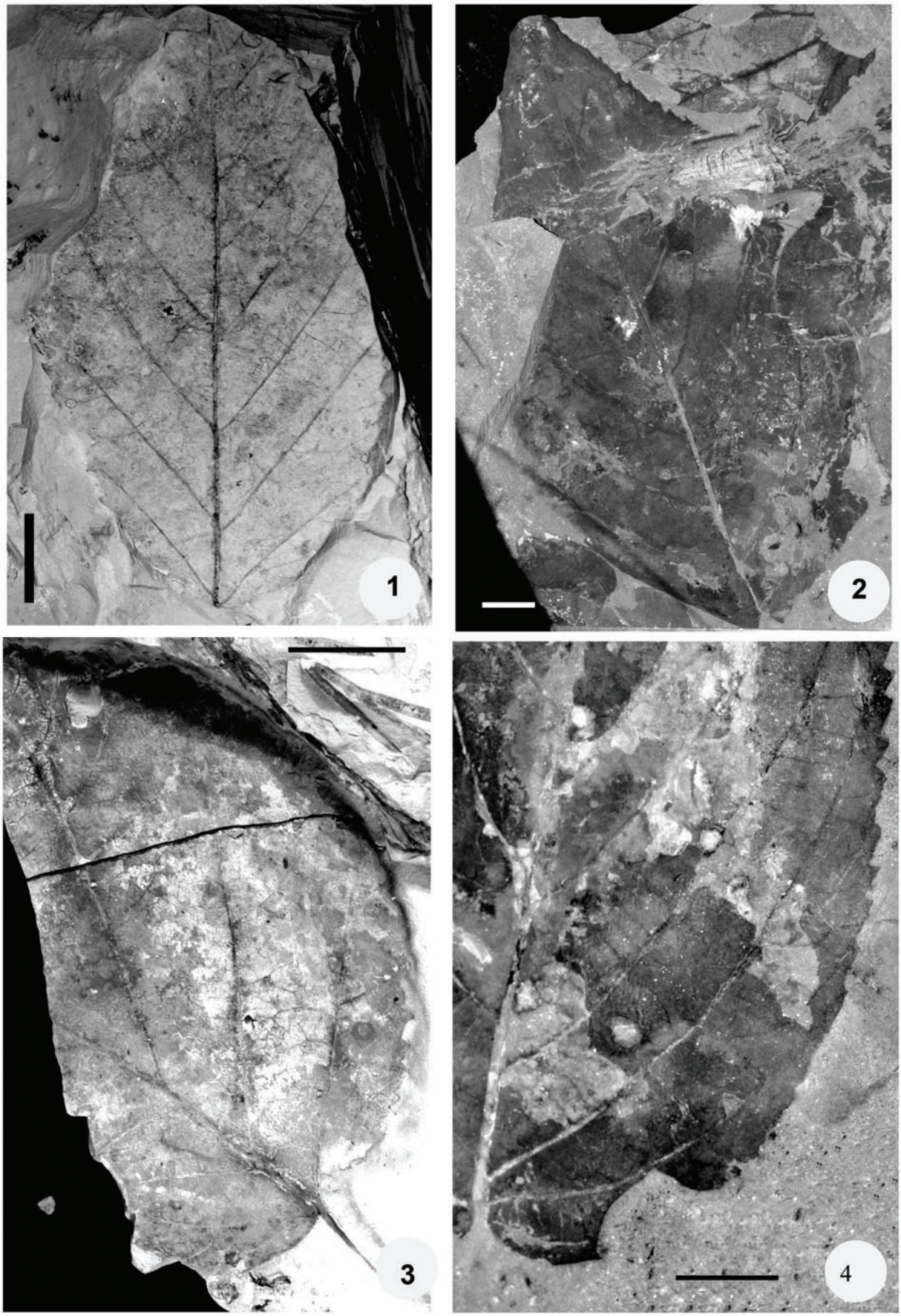


Plate 18

Plate 19

Figure 1. *Browneia serrulata* (Newberry) Manchester and Hickey, fruit, US817-9093. Scale bar = 1cm.

Figure 2-3. *Cornophyllum newberryi* (Hollick) McIver and Basinger.

Figure 2. Leaf, US822-9094. Scale bar = 1cm.

Figure 3. Leaf with complete petiole, US817-9095. Scale bar = 1cm.

Figure 4. *Davidia antiqua* (Newberry) Manchester, leaf, US820-9096. Scale bar = 1cm.

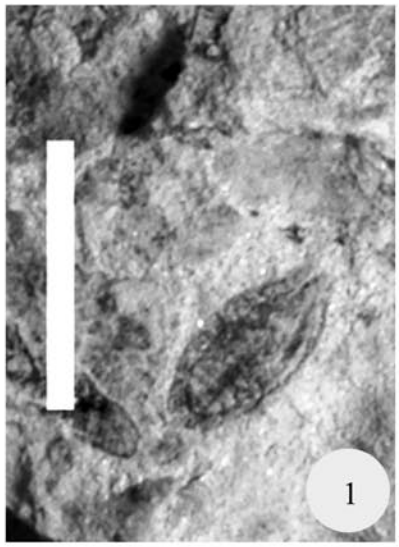


Plate 19

Plate 20

Figure 1. *Harmsvernia hydrocotyloidea* (McIver and Basinger) comb. nov., leaf, US826-9097. Scale bar = 1cm.

Figure 2-3. *Quereuxia angulata* (Newberry) Kryshtofovich.

Figure 2. Leaf, also numerous cf. *Azolla vellus* specimens, US845-9098. Scale bar = 1cm.

Figure 3. Leaf fragments, US845-9099. Scale bar = 1cm.

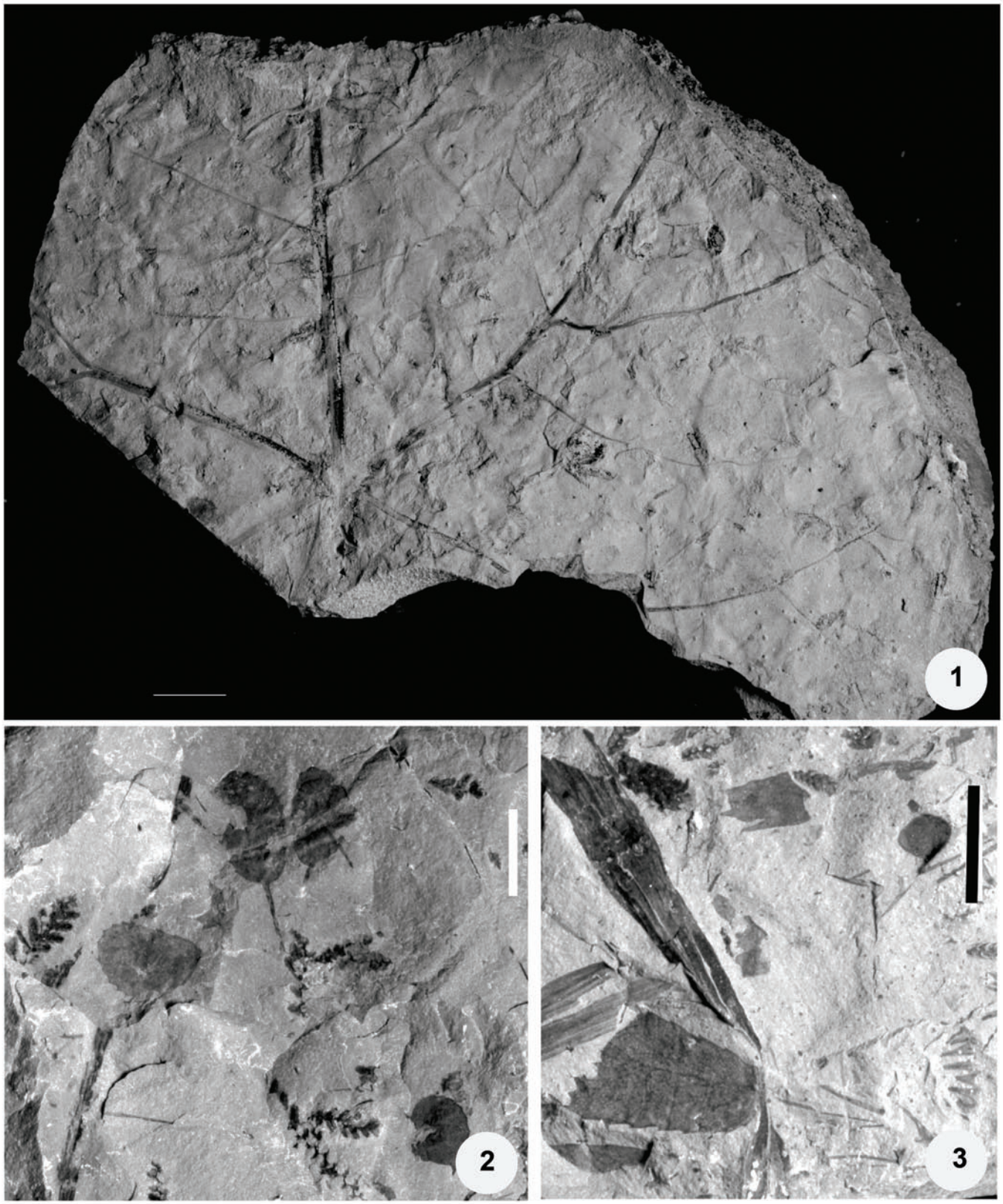


Plate 20

Plate 21

Figure 1. Unknown angiosperm 1, fruit or cone like structure, US822-9100. Scale bar = 1cm.

Figure 2-3 Unknown angiosperm 2.

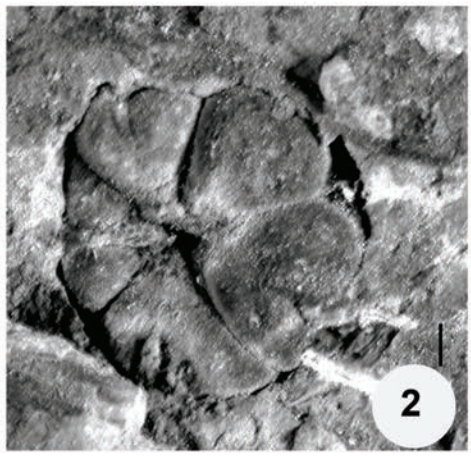
Figure 2. Fruit in longitudinal orientation, US828-9101. Scale bar = 1mm.

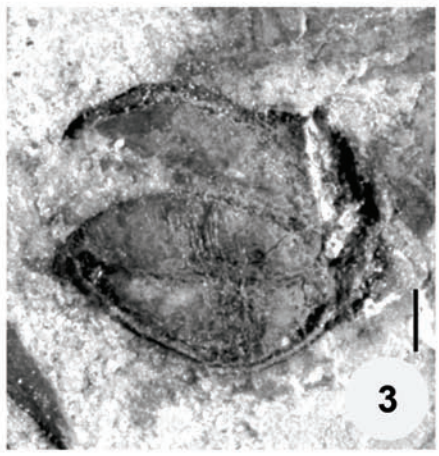
Figure 3. Fruit in lateral orientation, US828-9102. Scale bar = 1mm.

Figure 4. Unknown angiosperm 3, leaf, US836-9103. Scale bar = 1cm.

Figure 5. Unknown angiosperm 4, leaf fragment, US822-9104. Scale bar = 1cm.

Figure 6. Unknown angiosperm 5, unknown structure, US845-9105. Scale bar = 1cm.





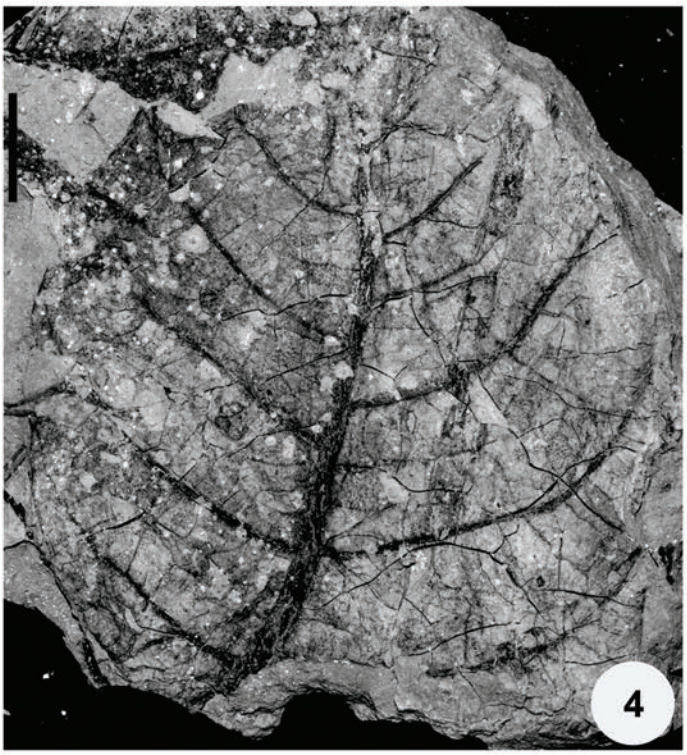


Plate 21

Plate 22

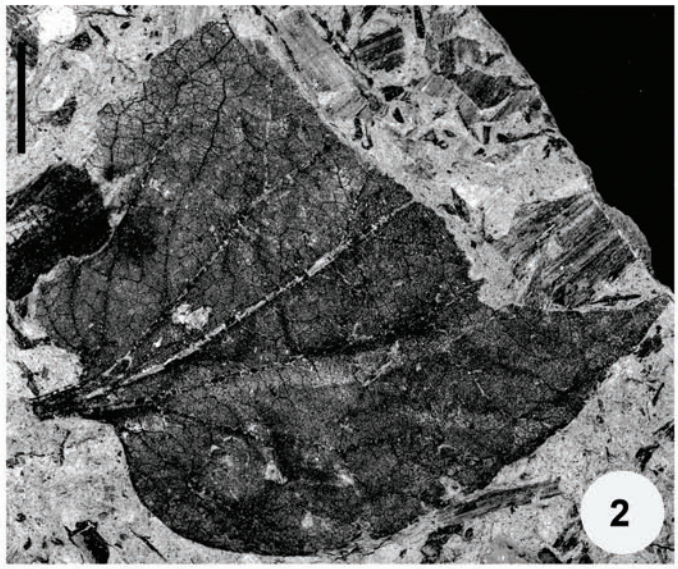
Figure 1. Unknown angiosperm 6, leaf, US828-9106. Scale bar = 1cm.

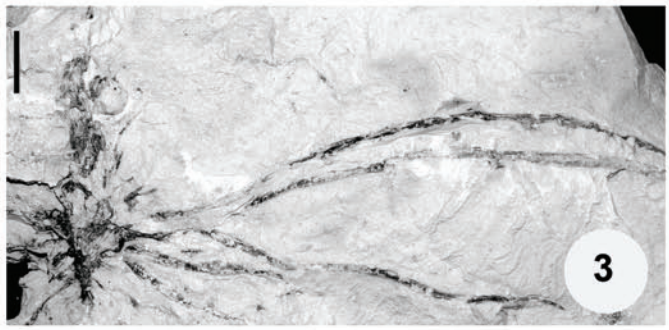
Figure 2. Unknown angiosperm leaf from 1992, US934-9107. Scale bar = 1cm.

Figure 3. Possible root structure, US832-9108. Scale bar = 1cm.

Figure 4. Vertebrate remains from a bone bed just below USPC loc. 833. Includes crocodile, gar, turtle. US833-9109. Scale bar = 1cm

Figure 5. Gastropod shell, US840-9110.





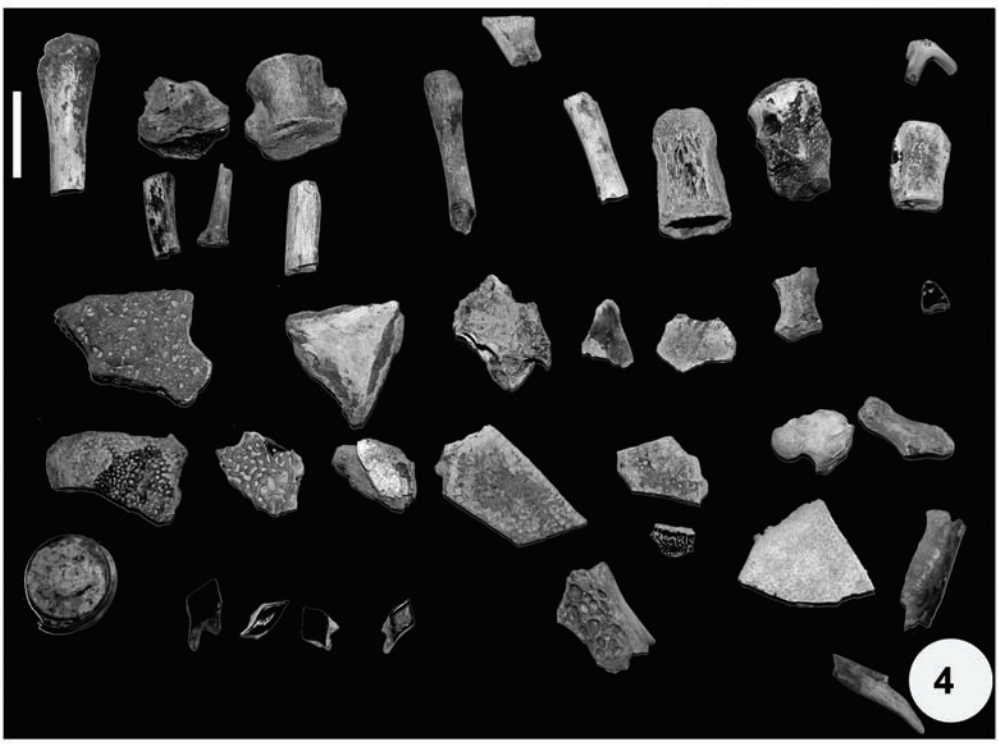


Plate 22